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An International Journal of Systematic Entomology

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See paper of **James K. Liebherr** *Cyphocoleus* Chaudoir (Coleoptera, Carabidae, Odacanthini): descriptive taxonomy, phylogenetic relationships, and the Cenozoic history of New Caledonia.

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Iuiuia caeca gen. n., sp. n., a new troglobitic planthopper in the family Kinnaridae (Hemiptera, Fulgoromorpha) from Brazil

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Abstract

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A new obligate cavernicolous (troglobitic) species in the planthopper family Kinnaridae is described from Brazil, and a new genus is established, as it could not be placed in any of the existing genera. Information on distribution and ecology is given. This is the second record of a troglobitic representative of this family from Brazil, and only the 6th cavernicolous kinnarid species worldwide.

Key Words

Taxonomy
troglobite
troglomorphy
caves
Neotropics

Introduction

A recent survey of limestone caves in the Iuiú municipality (Bahia state, Brazil) by a team of the Centro de estudos em Biologia Subterrânea, Federal University of Lavras, Brazil, revealed the existence of a previously unknown species belonging to the planthopper family Kinnaridae (Figs 1–2). The species displays conspicuous troglomorphic characters such as the absence of compound eyes and ocelli, reduction of tegmina and wings as well as body pigmentation, and is thus assumed to be an obligate cavernicole (troglobiont). Following the description of *Kinnapotiguara troglobia* (Hoch and Ferreira 2013, Xing et al. 2013), the new discovery represents the second record of a troglobitic kinnarid species from Brazil.

With currently 111 species in 21 genera, Kinnaridae is one of the smaller families within the Hemipteran group of Fulgoromorpha (Bourgoin 2015). Members of

the family are known to exist in the Old and New World (Bourgoin l.c.), with ca. 60 species documented to occur in the New World, predominantly in the Caribbean, North and Central America.

The epigean Kinnaridae fauna of Brazil, like that of South America in general, must be considered virtually unknown: hitherto only a single species has been documented, *Oeclidius parallelus* Muir, 1934 from Brazil.

Although information on the biology and ecology of Kinnaridae is largely lacking, the majority of the world's species are epigean and display well-developed compound eyes, vivid colouration of the body and tegmina, and are capable of flight. A few lineages, however, have colonized caves. Apart from *Kinnapotiguara troglobia*, described only recently from a limestone cave in Rio Grande do Norte State, NE Brazil (Hoch and Ferreira 2013, Xing et al. 2013), cave-dwelling kinnarid species have been reported from caves in Jamaica and Mexico: *Oeclidius antricola*

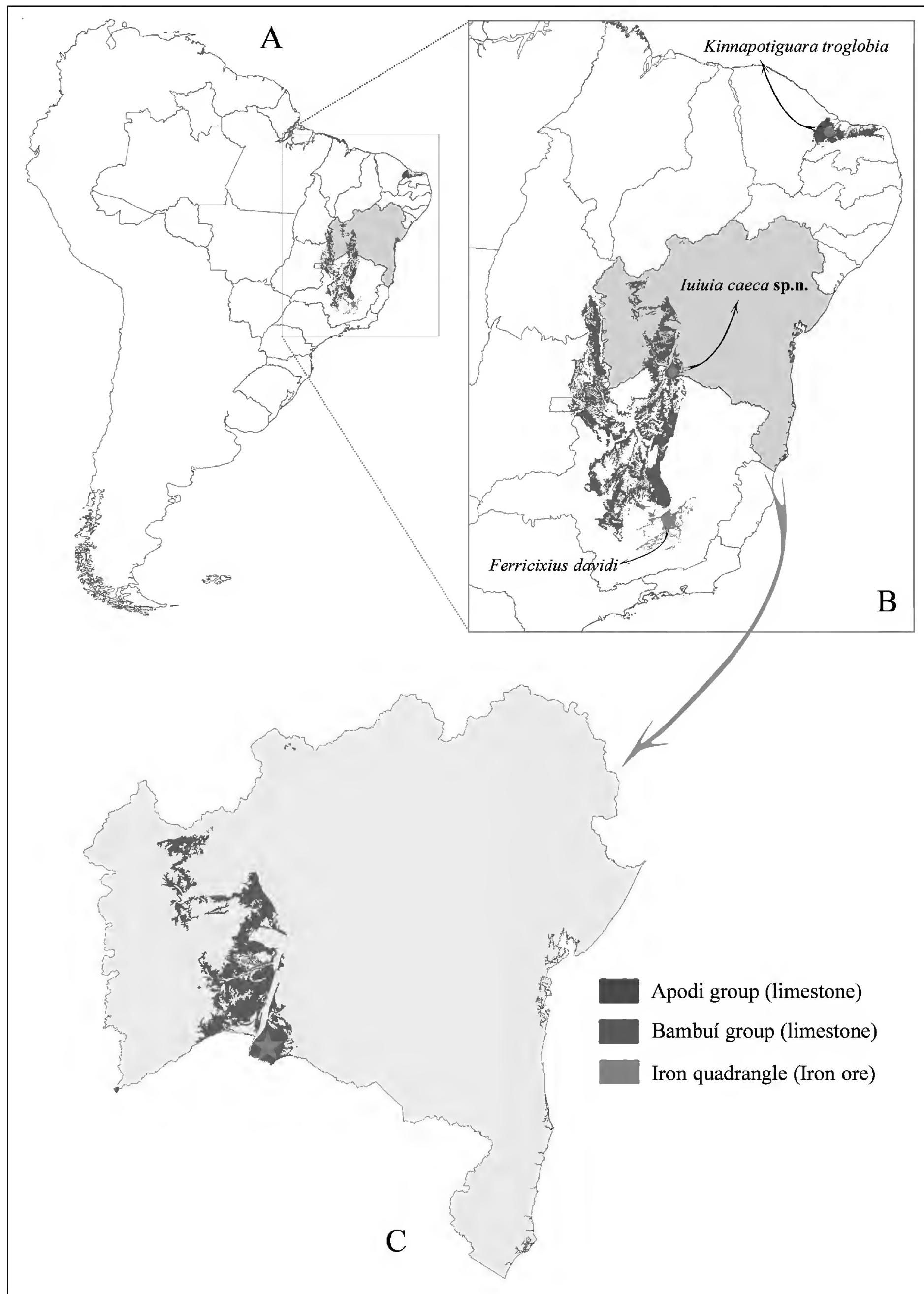


Figure 1. **A** Map of South America highlighting Brazilian states and three important speleological areas; **B** localities in Brazil where troglobitic planthoppers have been found; shaded area: Bahia State; **C** Bahia State, area enlarged, with limestone formations of the Bambuí group highlighted (blue).



Figure 2. **A** Surface vegetation near Toca do Baixão; **B** cave entrance, **C** *Iuiuia caeca* sp. n., adult male, on cave floor; **D** cave interior. Photographs by R.L. Ferreira.

Fennah, 1980, and *Oeclidioides minos* Fennah, 1980 (both troglobitic, Jamaica, occurring syntopic in Clarendon, Jackson Bay, Jackson Bay Cave), *Oeclidioides persephone* Fennah, 1980 (not conspicuously troglomorphic, except for the red pigmentation of the compound eyes; presumably troglophilic, from Jamaica, Clarendon, Portland Ridge, Portland Cave), and *Oeclidioides hades* Fennah, 1973 (troglomorphic, presumably troglobitic, from Mexico: San Luis Potosí, E. Valles, Cueva de Valdosa) (see Fennah 1973, 1980, Hoch and Ferreira 2013).

The classification of Kinnaridae is still under debate. Even Kinnaridae as a family has not yet been established as a monophyletic group. O'Brien and Wilson (1985:88) even stated that „the Kinnaridae may be difficult to identify“ and only Asche (1988: 51) mentioned the „comparatively broad costal field in the tegmen“ to be not only of diagnostic, but also of phylogenetic value. Bourgoin (1993) provided an initial phylogenetic hypothesis of a close relationship of the Meenoplidae and Kinnaridae based on a cladistic analysis. According to his hypothesis, Kinnaridae and Meenoplidae together would form a monophyletic group together, while the Kinnaridae should be regarded paraphyletic. Bourgoin (1993) considered the hypothesis as preliminary as taxon sampling was incomplete and additional character complexes needed to be examined.

Fennah (1945) subdivided Kinnaridae into the subfamilies Kinnarinae and Prosotropinae, and later provided a key to the New World genera, *Oeclidioides* and *Southia* Fennah (1980).

Kinnarinae were subdivided by Emeljanov (1984) into three tribes: Kinnarini, Propleromini and Adolendini. Emeljanov (1984: 52) placed the American representatives of the subfamily Kinnarinae, namely the genera *Oeclidioides* Van Duzee and *Southia* Kirkaldy, into the tribe Propleromini, limiting Kinnarini to the Old World taxa. More recently Emeljanov (2006) suggested an alternative tribal subdivision of the two subfamilies: Kinnarinae with a single tribe (Kinnarini) and Prosotropinae with four tribes (Prosotropini: New World, Kinnociini: Old World, Oecliini: New World, Adolendini (= Propleromini, = Emeljanopleromini: Koçak 1986): Old World).

Unambiguous synapomorphies have not been identified for any of the established genera or tribes. Thus the accommodation of the new species within any of the existing supraspecific taxa is inherently problematic.

Following the key provided by Emeljanov (2006) the new cavernicolous kinnarid from Brazil can be classified as a member of the subfamily Prosotropinae Fennah, 1945, and with some *caveat*, as a member of the – hitherto Old World – tribe Kinnociini (see Discussion: tribal placement).

In characters of the male genitalia, the new cavernicolous species does not share any similarities with any species of the known kinnarid genera (in or outside Kinnociini) which could be interpreted as synapomorphies. We thus opted for the establishment of a new genus which is described below.

Material and methods

Collecting, preservation, permanent storage. The specimens were collected by hand, and transferred immediately into vials containing 96% ethanol. For permanent storage, after dissection and examination, the abdomen and genitalia were transferred to polyethylene vials, and individually associated with the specimen vial.

Morphological examination techniques, visualization. Measurements and examinations of external body features were made from the specimen in ethanol, without further manipulation. To prepare male genitalia for dissection, the genital capsule was removed from the specimen, macerated for 24h in 10% KOH at room temperature, washed in water, transferred to glycerine for storage, or to glycerine-jelly for drawings. Examinations and drawings were made using a Leitz stereomicroscope with a *camera lucida* attachment.

Habitus photographs. The photograph in Fig. 3 was obtained from an image-stack taken with the aid of a Leica MZ 16 with a camera (Canon EOS 450D) attachment and Combine ZP software, and subsequently processed with Adobe Photoshop CS3. The photograph was taken from a specimen preserved in ethanol which had to be stabilized with fine-grained sand to obtain the desired strictly dorsal view.

Depository. ES: Laboratório de Ecologia Subterrânea/ISLA: Coleção de Invertebrados Subterrâneos da UFLA—Universidade Federal de Lavras, Brazil.

Taxonomy

Kinnaridae Muir

Kinnaridae Muir, 1925: 158
Prosotropinae Fennah, 1945: 449
Kinnociini Emeljanov, 2006: 1

Iuiuia Hoch & Ferreira, gen. n.

<http://zoobank.org/431A954A-B407-4242-84D0-A2F0ED93967D>

Type-species. *Iuiuia caeca* sp. n. (type locality: Brazil, Bahia State, Iuiu municipality).

Diagnosis. Small kinnarid (ca. 3 mm body length), strongly troglomorphic: compound eyes absent, tegmina reduced, wings vestigial, body pigmentation reduced (Fig. 3). *Iuiuia* gen. n. can be distinguished from all other kinnarid genera by the unique combination of the following characters: vertex wide and short; male genitalia with genital segment in caudal aspect approximately in a figure-8-shape; anal segment short, ventrally on each side with a distinct wing-shaped compressed process; parameres slender, narrow throughout, medially converging; aedeagus tubular, stout, periandrium with two large, lateral lobes. *Iuiuia* gen. n. differs conspicuously from *Kinnapotiguara* (Hoch & Ferreira, 2013) in the configuration of the male

genitalia (Hoch and Ferreira 2013: Figs 4, 5–10): genital segment with caudal margin smooth (vs caudal margin with lateral processes in *Kinnapotiguara*); anal segment with two short, wing-shaped lateroventral processes (vs anal segment with two pairs of slender processes in *Kinnapotiguara*); parameres narrow, slender throughout, medially converging (vs parameres differentiated into three processes in *Kinnapotiguara*) and aedeagus with two large lateral lobes (vs aedeagus without lateral processes in *Kinnapotiguara*).

Description. Head. Vertex trapezoidal, short, ca. 3 × wider posteriorly than medially long, with a very faint median carina; anterior and posterior margin of vertex parallel. Frons narrow, ca. 1.8–2.0 × longer than maximally wide, widest between level of antennae and frontoclypeal suture, ca. 1.3 × longer than post- and anteclypeus together, surface medially smooth, devoid of a median carina, lateral margins distinctly ridged. Frontoclypeal suture nearly straight. Post- and anteclypeus with a distinct median carina. Rostrum elongate, in repose well surpassing hind coxae, third joint shorter than second. Compound eyes absent, their former position recognizable by a shallow, vaulted area. Median (frontal) ocellus absent, lateral ocelli vestigial. Antennae with scape short, subcylindrical, slightly expanding distally; pedicel subcylindrical, ca. 2.4 × as long as wide, with distinct sensory plaque organs; arista ca. 2.8 × as long as pedicel.

Thorax. Pronotum tricarinate, ca. 3 × wider than vertex posteriorly, short, posterior margin medially shallowly concave; carinae distinct, median carina attaining but not surpassing anterior margin of pronotum; lateral carinae medially more or less parallel to posterior margin, and joining posterior margin laterally. Mesonotum faintly tricarinate, ca. 1.3 × wider than medially long. Tegulae vestigial. Hind tibiae laterally unarmed, distally with 7 slender teeth, arranged in a shallow arc. First metatarsal joint distally with 4/5 and 5/6, 2nd metatarsal joint with 3/4 or 4/5 teeth (individually and bilaterally variable). Pretarsal claws and arolia small, inconspicuous. Tegmina (Fig. 4) comparatively short, very shallowly tectiform, almost flat, in repose, in males either slightly shorter than tip of abdomen (parameres), or just reaching tip of abdomen, or slightly surpassing it; in females slightly shorter than tip of abdomen (dorsal margin of gonocoxae VIII); venation in proximal portion as in epigean Kinnaridae with a large and wide subcostal cell; clavus cixioid (*sensu* Emeljanov 1984), i.e., common claval vein (Pcu and A1) reaching hind margin of clavus (vein A2); basal cell of forewing closed by anastomosis of M and CuA, without conspicuous arculus; tegmen distally of nodal line distinctly reduced and variable among specimens with 6 distal marginal cells, partly incompletely delimited due to reduced distal marginal veins. Hind wings vestigial, very short, venation strongly reduced.

Male genitalia. Genital segment bilaterally symmetrical, in lateral aspect short, ca. 3 × as high as medially long; in caudal aspect approximately figure-8-shaped, in upper third laterally constricted, with a narrow transver-

sal bridge; anterior margin of genital segment smooth, without any conspicuous median apodemes; medioventral process prominent, broadly subtriangular, in lateral aspect distinctly exceeding caudal margin. Anal segment bilaterally symmetrical, short, stout, ventrally on each side with a compressed wing-shaped process. Parameres slender, narrow throughout, medially converging. Connective straight, narrow, almost terete.

Aedeagus bilaterally symmetrical, tubular, stout; periandrium with two large lateral lobes; proximal apodeme of aedeagus (= „tectiform structure“: term applied by Bourgoin 1997 for Meenoplidae) slender, with dorsal and ventral margins rapidly diverging, proximal margin rounded.

Females with abdominal tergites VI, VII and VIII bearing wax-fields. Female genitalia as in other Kinnaridae of the non-piercing type; sternite VII broadly rectangular, caudal margin straight; caudal margin of sternite VIII medially deeply incised; gonocoxae VIII bilobate, both lobes well developed, apically converging.

Etymology. The genus name refers to Iuiú, the name of the municipality where the cave (type locality) is situated. The gender is feminine.

Iuiuia caeca Hoch & Ferreira, sp. n.

<http://zoobank.org/841B93B6-AB8F-4D29-BD88-14EEBDC6DA34>
Figs 3–6

Diagnosis. Habitus (Fig. 3). Strongly troglomorphic species, predominantly yellowish body pigmentation, compound eyes and ocelli absent, dorsoventrally compressed body shape, tegmina short, in repose slightly surpassing tip of abdomen, wings vestigial.

Description. Body length. Measurements refer to distance between anterior margin of head to tip of abdomen (= caudal margin of parameres), those in brackets to distance of anterior margin of head to distal margin of tegmina.

Males. 2.8 (3.4)–3.8 (3.8) mm (n = 8). Females. 4.4 (4.0)–4.5 (4.1) mm (n = 2).

Colouration. Frons, vertex, pronotum yellowish, carinae contrasting dark brown; mesonotum more or less uniformly sordid yellowish; antennae and tegulae sordid light brown; tegmina translucent, uniformly yellowish-brown, veins slightly darker, without any conspicuous pattern. Metanotum, legs, as well as abdominal tergites and sternites pale yellow.

Configuration, shape and proportions of head and thorax as described for the genus.

Male genitalia (Fig. 5). Genital segment as described for the genus. Anal segment bilaterally symmetrical, short, in dorsal aspect subquadrangular, ventrally on each side with a wing-shaped, compressed lobe which is caudally rounded, cephally subacute and ventrally slightly curved medially. Parameres slender, medially concave, distally curved dorsomedially. Aedeagus bilaterally symmetrical, stout, tubular, central portion of periandrium distinctly constricted at ca. half its length, distally on its ventral side rapidly tapering into a helmet-shaped, bilobal



Figure 3. *Iuiuia caeca* sp. n. Habitus, male (holotype). Body length (apex of head to tip of abdomen) 2.8 mm. Photograph by M. Uhlig, Berlin.

structure with phallotreme apically; phallotreme in repose exposed dorsocaudally; perianthium smooth, without any spinose processes, but with two large lateral lobes which are ventrally broadly rounded, and dorsally – in their basal half – deeply concave.

External female genitalia (Fig. 6). Sternite VII in ventral aspect broadly rectangular, ca. 2.5 times as wide as long, lateral margins straight, more or less parallel, caudal margin smooth, more or less straight; sternite VIII in ventral aspect stout, in anterior portion ca. 3 times as wide as long, caudal margin medially deeply incised cephalically; gonocoxae VIII bilobate: ventral lobe in lateral aspect tongue-shaped and apically rounded, dorsal lobe more strongly developed than ventral lobe, distally tapering into an acute tip pointing medioventrally; both lobes beset with setae. Tergite IX narrow, dorsally short, laterally slightly expanding caudally. Anal segment (segment X) in dorsal aspect proximally narrow, distally expanding laterally, caudal margin in ventral aspect deeply concave. Anal style (segment XI) comparatively large, paraproct narrow, elongate, epiproct rounded, caudally not surpassing paraproct.

Distribution. The species is only known from the “Lapa do Baixão” cave in Iuiú municipality, Bahia State, Brazil. The external vegetation in the area corresponds to the “Caatinga” formation, the only xeric biome of the country, with xeromorph, deciduous vegetation (Fig. 2A). The cave has not been completely explored, since part of its inner chambers become flooded during rainy periods.

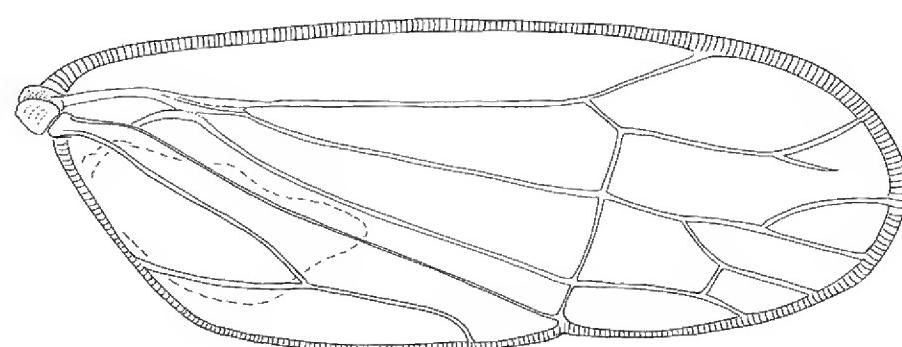


Figure 4. *Iuiuia caeca* sp. n. Left tegmen, male (paratype). Scale bar 0.1 mm.

However, the known passages extend over 500 meters. The only known entrance is a small opening (around 1 m² – Fig. 2B), which clearly imposes a huge stability to the cave atmosphere. During different surveys in the Iuiú municipality, another eight caves located near Lapa do Baixão cave were also sampled, but no specimen of *Iuiuia caeca* was found. This strongly suggests that the species is endemic to this cave. Furthermore, this cave was visited five times, and specimens were only found during two visits, which may suggest the low abundance of the species. However, during our last visit to the cave on 9.vii.2014, several adults and nymphs were observed, though they were restricted to a small part of the cave (see “Ecology”).

Geology. The “Lapa do Baixão” cave formed within limestones from the “Bambuí” geological group, from the Neoproterozoic, with ages ranging from 650–850 Myr. This group comprises the largest limestone formation in Brazil, embracing most of the known Brazilian limestone caves (Fig. 1). The other two troglobitic planthoppers described from Brazil are *Kinnapotiguara troglobia* (Hoch & Ferreira, 2013) (Kinnaridae), from limestone caves from the “Apodi” group (Rio Grande do Norte state), and *Ferricixius davidi* (Hoch and Ferreira 2012) (Cixiidae), known from a single iron ore cave in the “Iron quadrangle” formation (Minas Gerais state) (Fig. 1). The Apodi group comprises limestones from the Cretaceous (around 100 Myr), while the “Iron quadrangle” is much older (around 2.4 Byr).

Ecology. The Baixão cave possesses dozens of roots, mainly observed in the first portion of the cave (Fig. 2D). This part of the cave adjacent to the entrance comprises a labyrinth-like system of interconnected passages; then narrows into a single vadose and semi-meandrine passage. This deep vadose passage lacks roots, and no specimens of *Iuiuia caeca* were observed there.

Unfortunately, it was not possible to associate the roots to any particular plant species in the surface vegetation, but considering the distance between the surface and the cave, it appears likely that such roots belong to substantial trees with pivotant root systems, capable of penetrating deep inside the cracks into the soil and rock until reaching the cave chambers.

Such roots shelter a variety of invertebrate species which feed especially in their decomposing parts. However, also many non-troglobitic Cixiidae (*Pintalia* spp.)

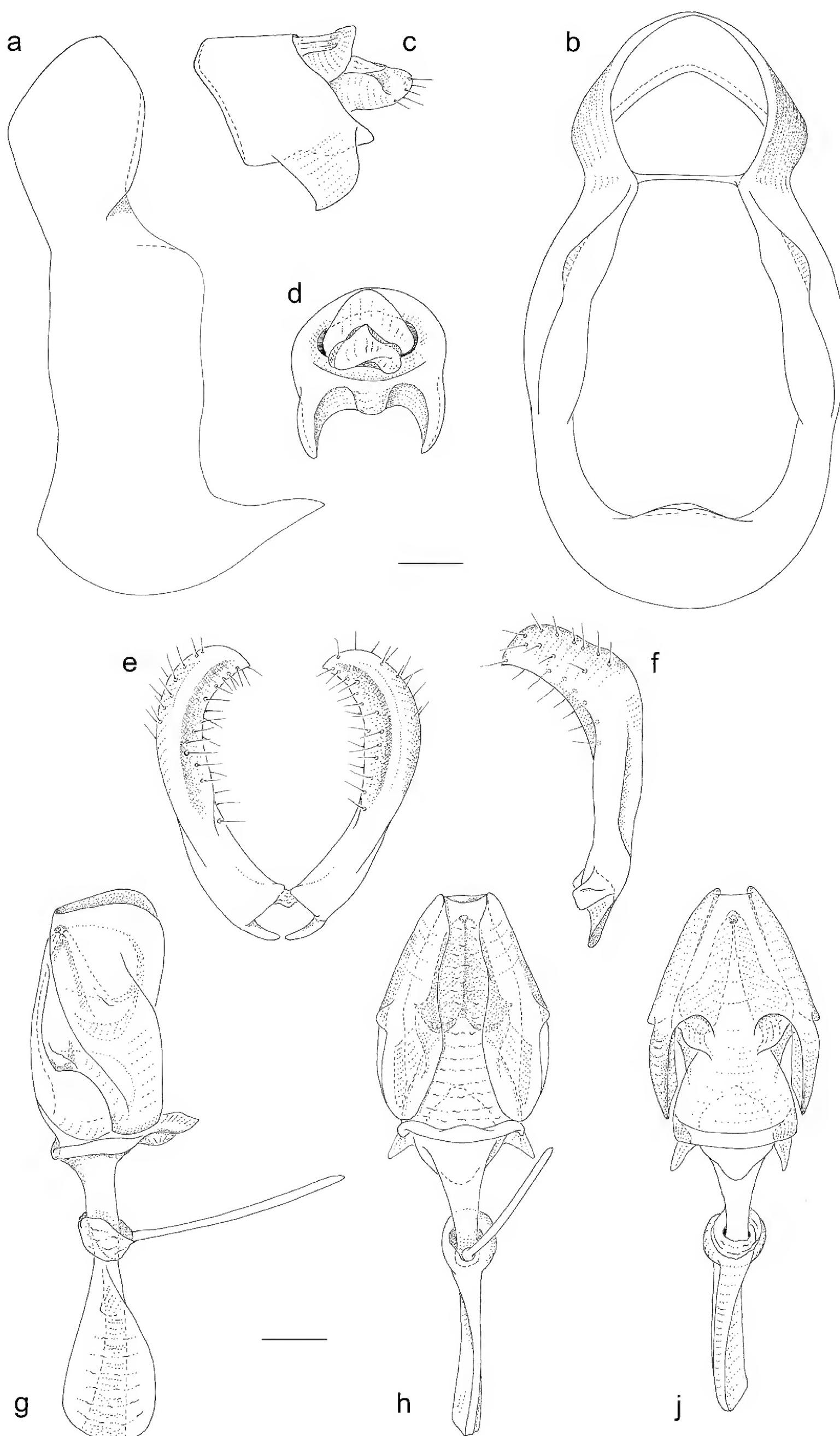


Figure 5. *Iuiuia caeca* sp. n. Male genitalia (paratype). **a** genital segment, left lateral aspect; **b** same, caudal aspect; **c** anal segment, left lateral aspect; **d** same, caudal aspect; **e** parameres, caudal aspect; **f** left paramere, left lateral aspect; **g** aedeagus with connective, left lateral aspect; **h** same, ventral aspect; **j** same, dorsal aspect. Scale bars: 0.1 mm.

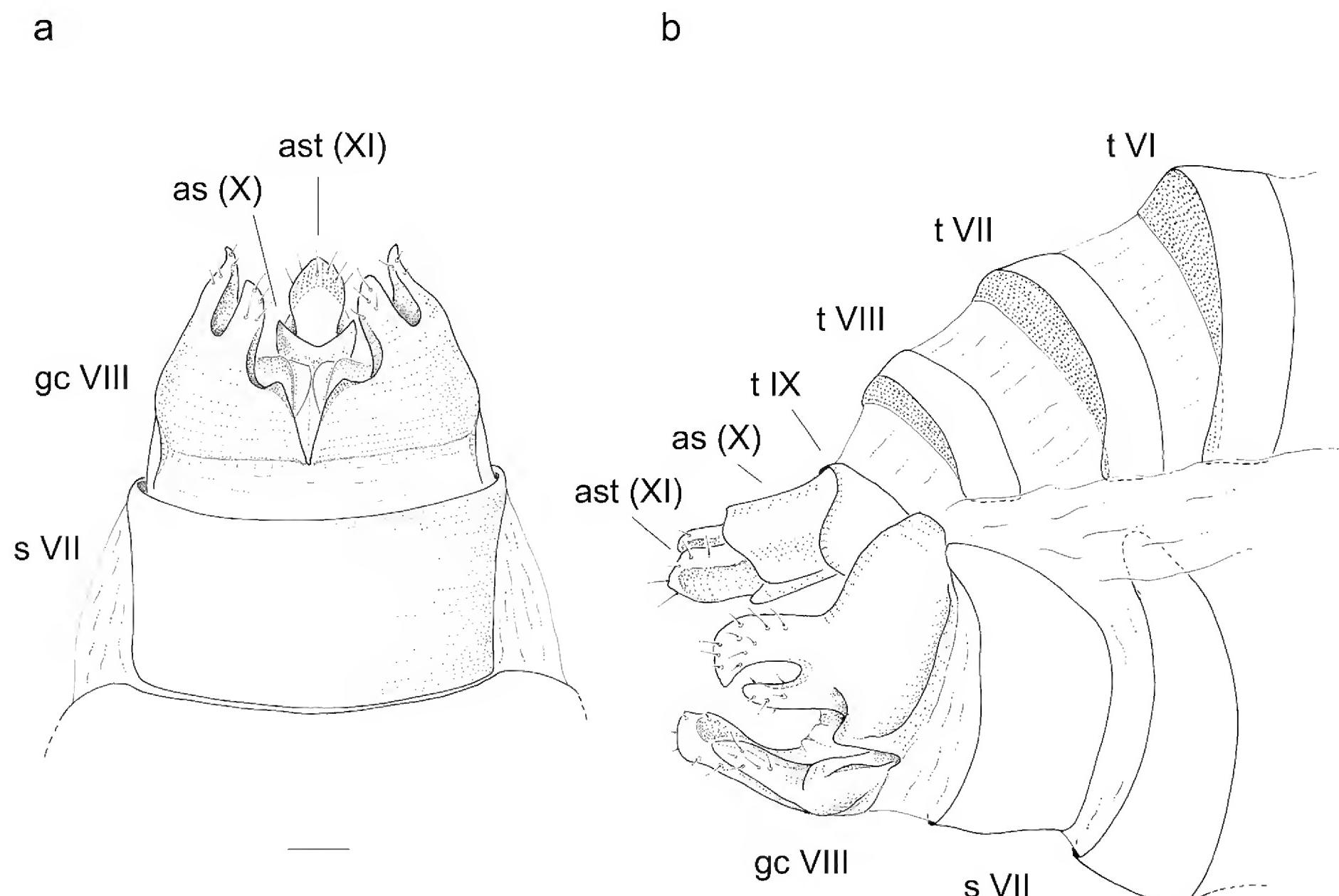


Figure 6. Female abdomen and external genitalia. **a** ventral aspect, **b** right ventrolateral aspect. Abbreviations: s VII = VII. sternite, gc VIII = gonocoxae VIII; as (X) = anal segment (X. segment); ast (XI) = anal style (XI. segment); t VI, t VII, t VIII = tergites of segments VI-VIII. Scale bar 0.1 mm.

feed on them, especially in those roots located nearer the entrance (but also in aphotic zones). These are supposedly accidentals to the cave, but eventually can become troglophiles. Specimens of *Iuiuia caeca* were observed only on roots within the labyrinthic part in the deep cave zone.

They were only rarely observed on the same roots where the non-troglobomorphic Cixiidae occur. The root mats where *Iuiuia* occur are mainly placed in the final portion of this labyrinthic part of the cave, near the connection with the inner single vadose and semi-meandrine passage. Such root mats are considerably smaller than those found in other parts of the cave. During a visit to the cave on 7.viii.2013, most of the observed specimens were nymphs, and only three adult males were found. During this visit, one of the males was found on a small root, near the cave floor, while the other two were found in an upper chamber, without roots, where they were freely walking on speleothems. During our last visit to the cave (9.vii.2014), seven adults and many nymphs were observed, but their spatial distribution was even more restricted. All observed specimens were associated with roots in a single part of the conduit, and no specimens were found in other chambers, as in the previous visit. Since both visits occurred in the dry period of the area, such differences observed on their abundance and distri-

bution cannot be primarily related to seasonal changes. Potential predators include spiders (especially Ochyroceratidae), Amblypygi (*Charinus iuiu* Vasconcelos & Ferreira, 2016) and a relatively large troglobitic pseudoscorpion species, with a body size of around 5 mm (*Spelaeobochica iuiu* Ratton, Mahnert & Ferreira, 2012); the latter is well distributed throughout the cave, but less common in the areas where *I. caeca* occurs.

Etymology. The species epithet “*caeca*” (blind, Lat.) refers to the complete reduction of compound eyes in this species. The gender is feminine.

Material examined. Holotype male. Brazil. Bahia State, Iuiu municipality, Toca Lapa do Baixão ($14^{\circ}23'8.13''S$, $43^{\circ}37'35.06''W$), 7.viii.2013, R.L. Ferreira leg., in coll. Universidade Federal de Lavras, ISLA.

Paratypes: 2 males, same data as holotype. 5 males, 2 females, same data as holotype, except 9.vii. 2014, in coll. Universidade Federal de Lavras, ISLA.

Remarks. In the cave, several 4th and 5th instar nymphs of Kinnaridae were collected which, due to substantial morphological differences, apparently represent two species. However, none of these nymphs could be associated with certainty to *Iuiuia caeca*. Thus it is likely that the cave Toca Lapa do Baixão houses at least two, if not three, kinnarid species.

Discussion

Tribal placement

The placement of *Iuiuia* into Kinnocciini ought to be considered preliminary as the characters observed in *Iuiuia caeca* do not fully coincide with those given by Emeljanov (2006) in support of his tribal concept. According to Emeljanov (2006), the Kinnocciini are characterized by the combination of the following characters: 1) metope (= frons) with complete or incomplete median carina, comparatively broad, its lateral carinae of moderate height; 2) integument dull, shagreened; 3) basal cell of fore wing closed by anastomosis of M and CuA; 4) wax-field in female on abdominal segments VI, VII and VIII. While *Iuiuia caeca* displays characters 3 and 4, there is a discrepancy in characters 1–2: the frons is smooth, without any median carina, and the integument is unpigmented. These characters, however, are often observed in obligately cavernicolous planthoppers (e.g., Hoch 1994, 2002, Howarth and Hoch 2005) and are likely to be the result of parallel evolution during adaptation to cave environments. The loss of compound eyes following the colonization of subterranean habitats is usually correlated with a broadening of the head, along with reduction of carinae (e.g., Hoch and Howarth 1989a, b), and bodily pigmentation is reduced, apparently due to altered physical properties in high humidity environments (e.g., Howarth 1983).

Thus it cannot be excluded that the closest epigean relative (whether extant yet unknown or extinct) displayed a median carinae of the frons and a darkly pigmented integument.

The genera currently featured in Kinnocciini, *Kinnoccia* Remane, 1985 and *Kinnocana* Remane, 1985 (as listed in Emeljanov 2006: 77) are distributed in the Old World, and endemic to the Canary Islands (Remane 1985). Placing *Iuiuia* into the Kinnocciini would extend the distribution of the tribe to the New World, and imply a biogeographical connection which may or may not reflect the evolutionary history of the taxon.

Epigean relatives

No close epigean relatives could be identified for *Iuiuia caeca* in Brazil, or elsewhere. The only epigean kinnarid species documented from Brazil is *Oeclidius parallelus* Muir, 1934, described from a single female from „Bahia; Iguassú“ (Muir 1934: 581), however, there is no indication of a closer relationship between *O. parallelus* and *I. caeca*. The similarity in external characters between *Iuiuia caeca* and the other troglobitic kinnarid from Brazil, *Kinnapotiguara troglobia* (Hoch & Ferreira, 2013) concerns troglomorphies and is thus the result of parallel evolution—the configuration of the male genitalia differs profoundly between the two species and does not support the assumption of a closer relationship and/or indicate a common ancestor.

The cave planthopper fauna of Brazil: evolutionary implications

It is certainly difficult to formulate a well-supported hypothesis regarding the evolution of the subterranean lineages of the Brazilian planthoppers, mainly due to the lack of knowledge on the epigean Fulgoromorpha fauna of Brazil. Different scenarios are conceivable, and may not be mutually exclusive. Initial cave adaptation may have occurred as a consequence of allopatric speciation following the extinction of epigean ancestral species as was postulated in the climatic relict hypothesis (Vandel 1964, Barr 1968) or may be the result of parapatric speciation by an adaptive shift of troglophilic populations to subterranean environments in order to exploit novel food resources (as suggested by Howarth 1981). For none of the cave planthoppers of Brazil, could close epigean ancestors be identified. They may not be known, or may even be extinct. Thus, all three known obligate cavernicolous planthopper species from Brazil must currently be regarded as relict species.

However, the structure and age of the rocks housing cave environments seem to be important factors acting on the evolution or at least on the distribution pattern of the cavernicolous Kinnaridae and Cixiidae of Brazil. Three biogeographic-geological constellations are observed:

- Iuiuia caeca* appears to be restricted to a single cave, which consists of a deep cave, which is possibly not connected to a larger system of mesocaverns.
- Populations of the kinnarid *Kinnapotiguara troglobia* are known from many caves in the Apodi group in the Rio Grande do Norte State (Hoch and Ferreira 2013). The species is associated with shallow caves which appear to be interconnected by several mesocaverns consisting of cracks and faults (Hoch and Ferreira 2013). This might explain the wide distribution of this species. Further research must show, however, whether differentiation (genetic or behavioral although not-yet-morphological) occurs between these populations.
- Ferricixius davidi*, the only troglobitic Cixiidae known for Brazil, is found in a single iron ore cave, located in an area where hundreds of caves are known. This cave is very close to the surface, and roots penetrate into the subterranean macrocaverns. The cave is also interconnected with other caves in the surroundings by small canaliculi present on the topmost ferruginous breccia, which would theoretically allow migration between caves, so long as a suitable microhabitat (e.g., high relative humidity, food resources) is maintained.

Conservation status

The external area surrounding the cave is heavily impacted, mainly by human activities such as agriculture and extensive breeding of cattle and goats. Moreover, the area is currently being evaluated for its potential for limestone extraction. Hence, although there are no mining activities yet in the area, such activities will probably start in a near future, posing a potential risk to the cave environment. A

new railway (FIOL–Ferrovia de Integração Oeste-Leste) that is being constructed connecting the Brazilian coastal area to this inner portion of Bahia state will favour the outflow of feedstock (especially agricultural products and ore), which will certainly contribute to arising the interest of exploiting the limestone in the area. Fortunately, the cave did not show any indication of human visitation, thus we consider the best option for the moment in order to preserve the cave may be to not publicly disclose the precise GPS data of its location.

It is worth mentioning that the Lapa do Baixão cave has many other troglobitic species (12 species) from which only two are currently described: *Spelaeobochica iuiu* Ratton, Mahnert & Ferreira, 2012 (Pseudoscorpiones, Bochicidae) and *Iuiuniscus iuiuensis* Souza, Ferreira & Senna, 2015 (Isopoda, Styliniscidae). Therefore, *Iuiuia caeca* comprises the third troglobitic species described from this cave, which certainly deserves attention regarding its conservation. Many hotspots of subterranean biodiversity (those caves or cave systems with 20 or more cave obligate species) (Culver and Sket 2010) occurs around the world, but currently there are no such hotspots in South America. In most cases, the high number of troglobitic/stygobitic species depends on the sampling efforts spent in a given cave.

Accordingly, Toca do Baixão cave certainly has potential to become a hotspot in the future, since only a few samplings were conducted there. Therefore, it is crucial that Brazilian government earmark some conservation efforts to preserve this unique cave and its endemic inhabitants.

Brazil – hotspot of cave planthopper diversity?

The discovery of *Iuiuia caeca* not only represents the 3rd obligate cavernicolous Fulgoromorpha species in Brazil, but also provides evidence of three separate evolutionary lineages which have invaded caves, two within the Kinnaridae, and one within the Cixiidae. All three species were discovered within a few years and are the result of the exploration efforts of a single, but active team of speleologists. Given the vast extension of cavernous substrate in Brazil and the availability of suitable planthopper habitat, Brazil may soon join Hawaii (e.g., Fennah 1973a, Hoch and Howarth 1999, Wessel et al. 2013), Australia (e.g., Fennah 1973b, Hoch and Howarth 1989a, b, Hoch 1990, 1993) and the Canary Islands (e.g., Remane and Hoch 1988, Hoch and Asche 1993, Hoch et al. 2012) as another hotspot for cave planthopper diversity. It is to be hoped that legal measures for the conservation of the subterranean fauna of Brazil—which constitutes one of the country's unique biological resources—will be developed and consequently reinforced.

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Workers, soldiers, and gynes – morphometric characterization and description of the female castes of *Camponotus singularis* (Smith, 1858) (Hymenoptera, Formicidae)

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Abstract

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Species of *Camponotus* Mayr, 1861 show a high variation of worker caste numbers, from a monomorphic worker caste to strong polymorphism along a continuous range of worker sizes or true worker dimorphism. *Camponotus singularis* (Smith, 1858) is used as a model for a *Camponotus* species with two very distinct worker castes (minors and majors) which are chiefly defined by morphometric data. We investigated shifts in proportions of *C. singularis* female castes in order to identify major allometric patterns useful for characterizing caste differences in this species as well as in other Camponotini. We describe the main morphological traits which are characteristic for the respective morphs. The major worker, or “soldier”, shows many characteristics which deviate from the minor worker, but also from the alate gyne. Its traits are assumingly modified for its function in nest defence. Morphometric data clearly set Bornean specimens of *Camponotus singularis* (described as var. *rufomaculatus* Donisthorpe, 1941) apart from specimens with other provenances, suggesting that this island population is a distinct species.

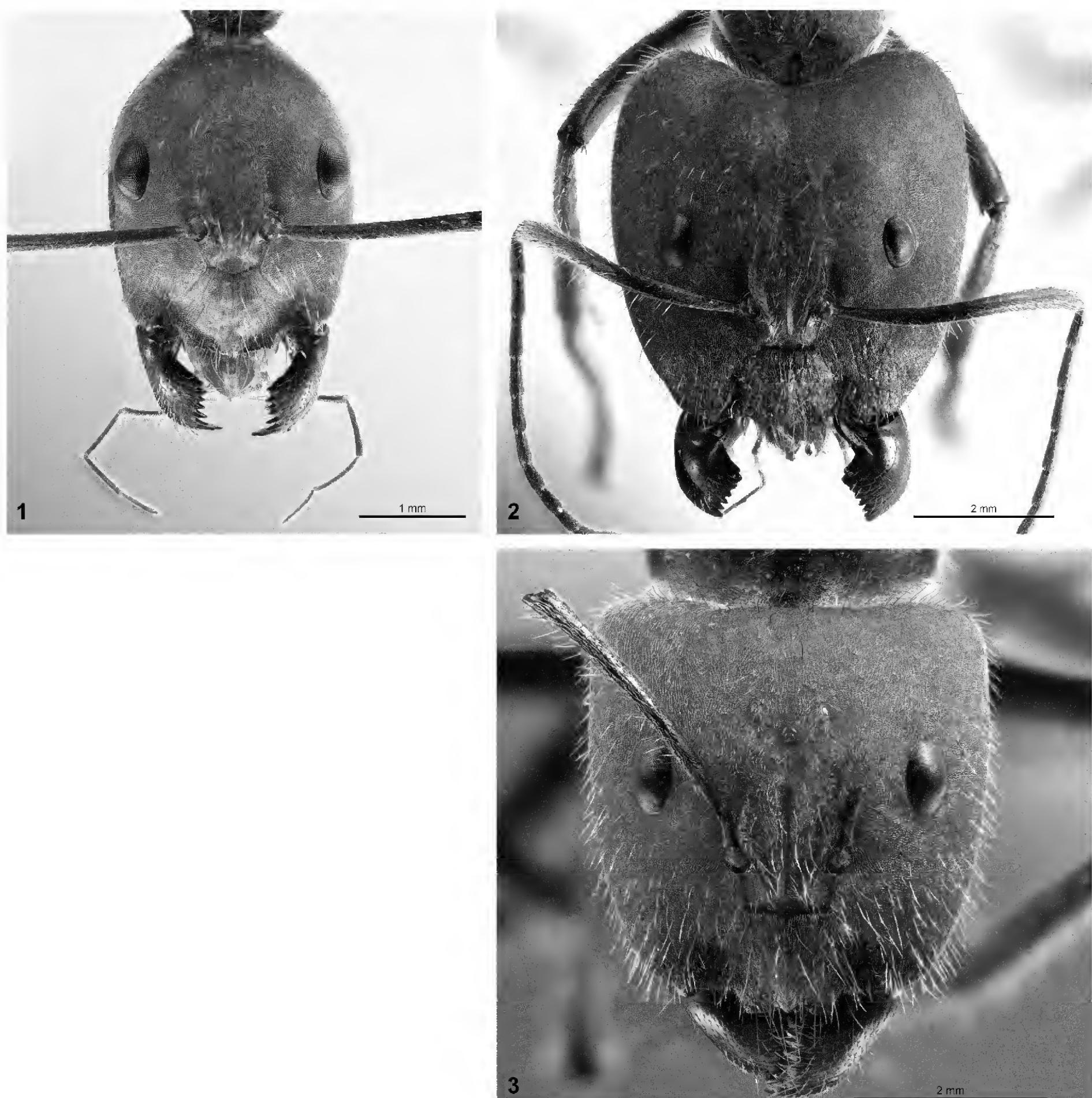
Introduction

Within the eight recent genera of the tribe Camponotini (Blaimer et al. 2015, Ward et al. 2016), the worker caste is developed in a variety of forms, comprising species with monomorphic (e.g., *Polyrhachis* Smith, 1857; Dorow 1995), continuously polymorphic (e.g., some species of *Camponotus* Mayr, 1861; Wilson 1953, Busher et al. 1985) and dimorphic workers (e.g., *Colobopsis* Mayr, 1861). Even the most speciose genus, *Camponotus*, exhibits all known types of worker polymorphism: from species with monophasic allometry to those with true worker dimorphism (Wilson 1953).

During our ongoing revision of the *Colobopsis cylindrica* group, which includes a morphometric analysis of species, a review of previous publications revealed multiple mentions of poly- or dimorphism in workers of Cam-

ponotini (e.g., Wilson 1953, Baroni Urbani 1974, Busher et al. 1985), but a comparatively small number of more recent studies focusing on morphometry (e.g., Diniz-Filho et al. 1994, Rakotonirina et al. 2016).

We herein present morphometric data on the Asian species *Camponotus singularis* (Smith, 1858), a large-bodied species with a wide distribution from Nepal to Borneo and Java (e.g., Smith 1858, Chapman and Capco 1951, Thapa 2000, Jaitrong and Nabhitabata 2005, Guénard and Dunn 2012, Bharti et al. 2016). We have chosen this taxon, because it serves as an example of a species with a clear worker dimorphism, most apparently characterized by the size and shape of the head, and without the occurrence of intermediate phenotypes. We describe the differentiating characters of the two worker castes (minors, majors) and compare them to the corresponding characters of the gynes (see Figs 1–6). Molet



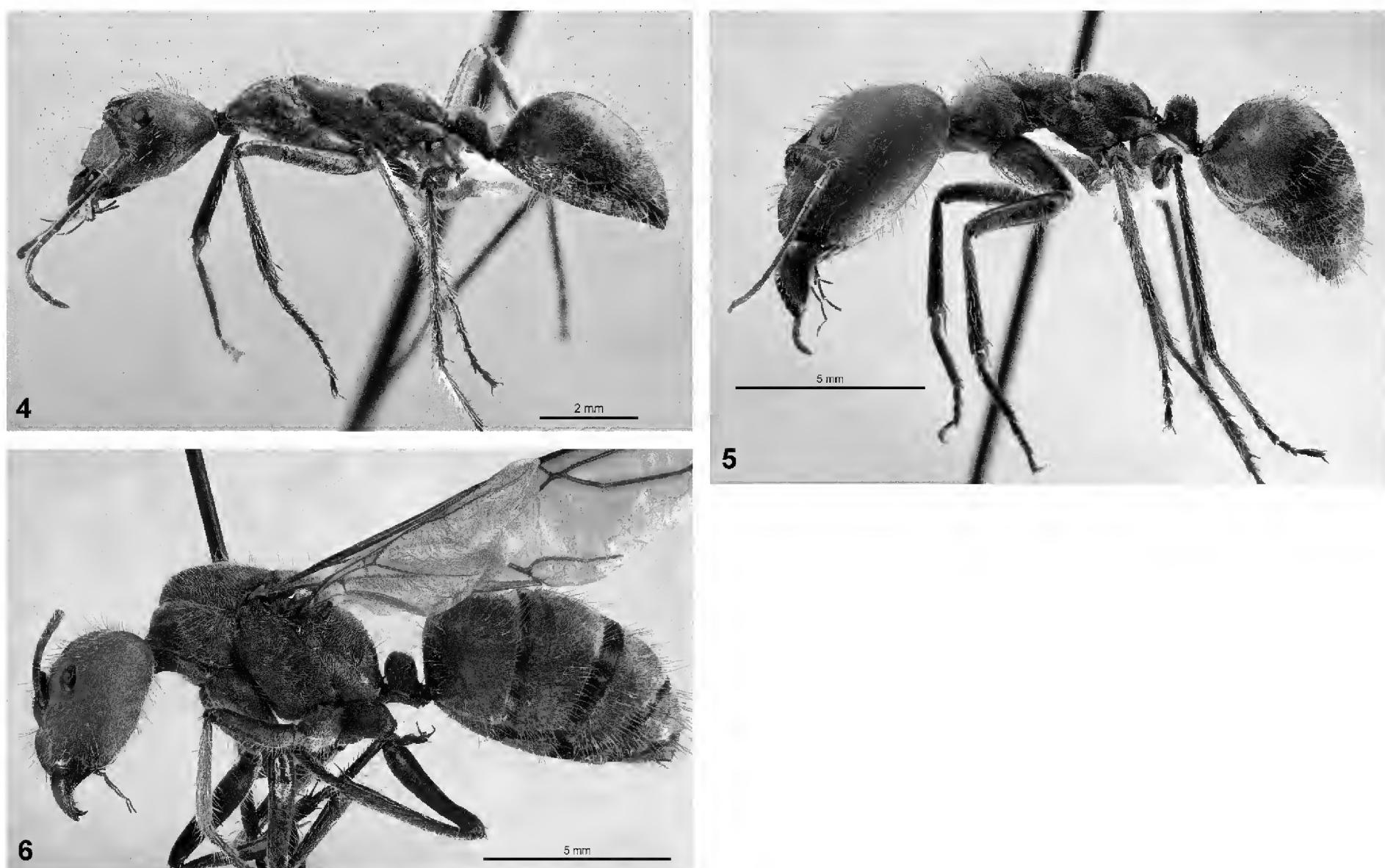
Figures 1–3. *Camponotus singularis*, head, frontal view, of (1) minor worker, (2) major worker, and (3) gyne. Notably different are head shape, development of posterior margin, and position of eyes. The minor has much longer scapes and maxillary palpi than the major.

et al. (2012, 2014) interpret specialized castes as mosaics of pre-existing phenotypes with novel or “recycled” developmental pathways. Building on this evolutionary model, we aim to characterize major and minor workers as two distinct subcastes based on their morphological proportions. Although morphometric differences in Camponotini may vary from clade to clade, within this study we attempt to identify representative caste-specific allometric patterns which may not only be applicable to the dimorphism of *C. singularis* but also serve to characterize caste-polymorphism in other camponotine ants.

Material and methods

Specimen depositories

BMNH	Natural History Museum, London, United Kingdom
CAS	California Academy of Sciences, San Francisco, USA
CZW	Coll. H. Zettel, Vienna, Austria
MCSN	Museo Civico di Storia Naturale Giacomo Doria (main collection and Carlo Emery’s collection), Genova, Italy



Figures 4–6. *Camponotus singularis*, lateral view, of (4) minor worker, (5) major worker, and (6) gyne. Notable are differences between the worker subcastes regarding head size, mesosoma height, and petiole shape. Mesosoma and gaster of the gyne are strongly enlarged for flight and reproduction.

NHMW	Natural History Museum Vienna, Austria
SKYC	Sk. Yamane Collection, Korimoto, Japan
THNHM	Thailand Natural History Museum, Phatum-thani, Thailand
VNMN	Vietnam National Museum of Nature, Hanoi, Vietnam

Material examined

We measured specimens from most parts of the distribution area of *C. singularis*, except from Nepal and India. In total five gynes, ten major workers and 85 minor workers of *C. singularis*, as well as five minor workers and one gyne of *C. singularis* var. *rufomaculatus* Donisthorpe, 1941 were examined. During data processing we noticed that specimens from Borneo differed clearly from specimens collected in other localities. Consequently, we removed Bornean specimens from our in-depth analysis of morphs, but present some data on how to differentiate this population.

Camponotus singularis, typical form: **Myanmar**: 1 minor worker (BMNH), Mandalay Region, Pyin U Lwin, ca. 900 m a.s.l., V.1899, coll. Bingham [*Camponotus camelinus* Smith, Upper Burma Maymya, 3000 ft, 5.1899, Bingham coll.]; 1 major worker, 1 minor worker (MCSN), Kayin State, mountains east of Toungoo [Carin Cheba], 900–1100 m a.s.l., V.1888, leg. L. Fea; 1 minor worker (MCSN), Kayin State, Kawkareet, I–II.1887, leg. L. Fea; 1 major worker, 2 minor workers (MCSN, NHMW), Kayin

State, [“Tenasserim”], Thagata, IV.1887, leg. L. Fea; 1 minor worker (MCSN), Tanintharyi Region, [“Tenasserim”], Malewoon, VII–VIII.1887, leg. L. Fea. – **Thailand**: 1 minor worker (BMNH), Chiang Mai [Chiengmai], 19.I.1936, Lot 317/94; 1 minor worker (NHMW), Thailand, Satun Province, Thale Ban National Park, 10–16. III.1993, leg. M. Madl; 1 minor worker (BMNH), Pattani Province, Bukit Besar near Amphoe Nong Chik (for interpretation see Woodley 2012), ca. 900 m a.s.l., 1903, leg. Annandale & Robinson [Bulsit [sic!] Besar, Siam: Malay States, No. 12, 3000', Annandale & Robinson, Siamese Malay States 1903-127, *Camponotus camelinus* Sm. Donisthorpe det.]; 1 minor worker (THNHM), Chiang Rai Province, Mae Pha Laung District, 20.VI.2002, leg. W. Jaitrong; 1 minor worker (THNHM), Pattalung Province, Khao Pu – Khao Ya National Park, Reang Tong Waterfall, evergreen forest, 28.IX.2007, leg. P. Kosonpanyapiwat; 1 minor worker (THNHM), Ranong Province, Khlong Naka Wildlife Sanctuary, evergreen forest, 12.VIII.2009, leg. W. Jaitrong. – **Laos**: 6 minor workers (NHMW), Luang Nam Tha Province, 5–10 km SW of Muang Sing, 600 m a.s.l., 11.VI.1996, leg. H. Schillhammer (#23); 1 major worker (NHMW), Luang Nam Tha Province, ca. 20 km SE of Muang Sing, 950 m a.s.l., 12–13.VI.1996, leg. H. Schillhammer (#25); 1 major worker (NHMW), Luang Nam Tha Province, ca. 10 km E of Muang Sing, 600 m a.s.l., 19.VI.1996, leg. H. Schillhammer (#32); 1 major worker, 40 minor workers (CZW), Hua Phan Province, Ban Saleui, Phou Pan (Mt.), 1300–1900 m a.s.l., 20°12'N 104°01'E,

7–29.IV.2014 (various dates), leg. C. Holzschuh. – **Vietnam:** 1 minor worker (VNMN), Lao Cai Province, Van Ban, ca. 150 m a.s.l., 4.VI.2005, leg. B.T. Viet (#Code I). – **West Malaysia:** 1 minor worker (CZW), West Malaysia, Kelantan, 60 km NE Tanah Rata, Tanah Kerajaan, 1000 m a.s.l., 12–30.IV.2007, leg. P. Cechovsky; 3 minor workers (CZW), West Malaysia, Kelantan, 30 km NW Gua Musang, Ulu Lalat, Kpg. Sungai Om, 800–1000 m a.s.l., 21.VI.–14.VII.2010, leg. P. Cechovsky; 2 minor workers (CZW), West Malaysia, Perak, 25 km NE Ipoh, Banjaran Titi Wangsa mts., Korbu (Mt.), 1200 m a.s.l., 11.–16. I.1999, leg. P. Cechovsky; 1 major worker, 8 minor workers (CZW), West Malaysia, Perak, 30 km SE Ipoh, Cameron Highland, Ringlet, 900 m a.s.l., 25.IV.–5.VI.2001, leg. P. Cechovsky; 1 minor worker (CZW), West Malaysia, Perak, 40 km SE Ipoh, Banjaran Titi Wangsa mts., Ringlet, 900 m a.s.l., 25.III.–3.IV.2002, leg. P. Cechovsky. – **Indonesia:** 2 minor workers (NHMW), Sumatra (#877-2); 1 minor worker (NHMW), Sumatra, 1875, leg. Plason; holotype minor worker (BMNH), Java (# 55, 39), “*F. singularis* Sm., Type”, CASENT0903554; 5 alate gynes (NHMW), Java, leg. Adensamer; 1 major worker, 1 minor worker (NHMW), Java, leg. Vollenhov; 1 minor worker (NHMW), Java, 1874, leg. Plason; 2 minor workers (MCSN), Java, Kota Bogor [Buitenzorg], 1875, leg. G.B. Ferrari; 1 minor worker (MCSN), Java, Kota Bogor [Buitenzorg], IV.1876, leg. Beccari; 1 major worker (SKYC), Java, Kota Bogor, 3–5.XI.1985, leg. Sk. Yamane; 1 minor worker (SKYC), Java, G. Sarak, near Kota Bogor, 8.III.1997, leg. Sk. Yamane; 1 minor worker (CAS), Java, Kota Bogor, Botanical Gardens, 16.XII.1978, leg. E. S. Ross. – **Unknown localities:** 1 major worker, 1 minor worker (NHMW), coll. Felder; 1 major worker (NHMW), unknown collector.

Camponotus singularis var. *rufomaculatus*: **East Malaysia (Borneo):** 2 minor workers (MCSN), Sarawak, 1865–1866, leg. G. Doria; 1 minor worker (SKYC), Sabah, Crocker Range, Inobong (forest), 500–600 m a.s.l., 26.II.2008, leg. Sk. Yamane; 1 dealate gyne (SKYC), Sabah, Sipitang, Muaya Forest Reserve, 700 m a.s.l., 28.VIII.2012, leg. Sk. Yamane; 1 minor worker (SKYC), Sarawak, Kubah National Park, 5.XII.1993, leg. Sk. Yamane; 1 minor worker (SKYC), Sarawak, Engkari, Ubah Ribu, 23.IV.1994, leg. K. Het.

Examined specimens were either pinned or dry mounted on card squares or triangles. Examination and measurements of specimens were carried out with a Nikon SMZ1500 binocular microscope at magnifications of up to 256×.

Measurements and indices

- | | |
|----|---|
| TL | Total length. The added lengths of head (including mandibles), mesosoma, petiole, and gaster. |
| HW | Head width. Maximum width of head in full-face view, excluding eyes if laterally protruding (few minor workers). |
| HL | Head length. Maximum length of head in full-face view, excluding mandibles, measured parallel to midline from anterior-most point of cly- |

peus to midpoint of occipital margin (in minor workers) or to midpoint of an imaginary line connecting the apices of posterior projections (major workers and some gynes).

HS	Head size. $(HW+HL) / 2$.
EL	Eye length. Maximum diameter of compound eye.
SL	Scape length. Maximum length of antennal scape in dorsal view excluding basal neck and condyle.
ML	Mesosoma length. Measured laterally from anterior surface of pronotum proper (excluding collar) to posterior extension of propodeal lobes.
PH	Petiole height. Maximum height of the petiole in lateral view, measured from ventral-most point of petiolar sternum to dorsal apex.
PL	Petiole length. Maximum length of petiole in lateral view, measured from inflexion point of anterior constriction to posterior margin.
NH	Node height. Height of petiolar node, measured laterally, from the intersection point of the axes of maximum height and length to dorsal apex.
FeL	Femur length. Maximum length of hind femur, measured from base to apex.
PS5	Length of maxillary palp segment 5, measured from base to apex.
PS6	Length of maxillary palp segment 6, measured from base to apex.
CI	Cephalic index. $HW / HL \times 100$.
SI	Scape index. $SL / HW \times 100$.
EI	Eye Index. $EL / HW \times 100$
PI	Petiole Index. $PH / PL \times 100$
FeI	Femur Index. $FeL / HW \times 100$
PSI	Palp Segment Index. $(PS5+PS6) / HS \times 100$

All measurements are in millimetres and separated by caste. Due to the condition of some specimens, not all measurements were taken from all animals. Measurements of minor workers include the holotype (plotted separately in Figs 9, 12, 14). The total number of specimens measured is given for each morph (n), deviating numbers for individual characters are written in parentheses. The raw data set of all measurements is available as an electronic supplement (Suppl. material 1).

Digital photos were taken with a Leica DFC camera attached to a Leica MZ16 binocular microscope with the help of Leica Application Suite V3, and stacked with ZereneStacker 64-bit. Processing of images was performed with Adobe Photoshop 7.0.

Results

Dimorphism of workers of *Camponotus singularis* (typical form):

Body size:

Measurements: alate gynes (n = 5): TL 18.42–20.48 (4); ML 6.52–6.78; major workers (n = 10): TL 16.76–19.57; ML 5.22–6.07; minor workers (n = 85): TL 9.26–15.39; ML 3.85–5.28 (84).

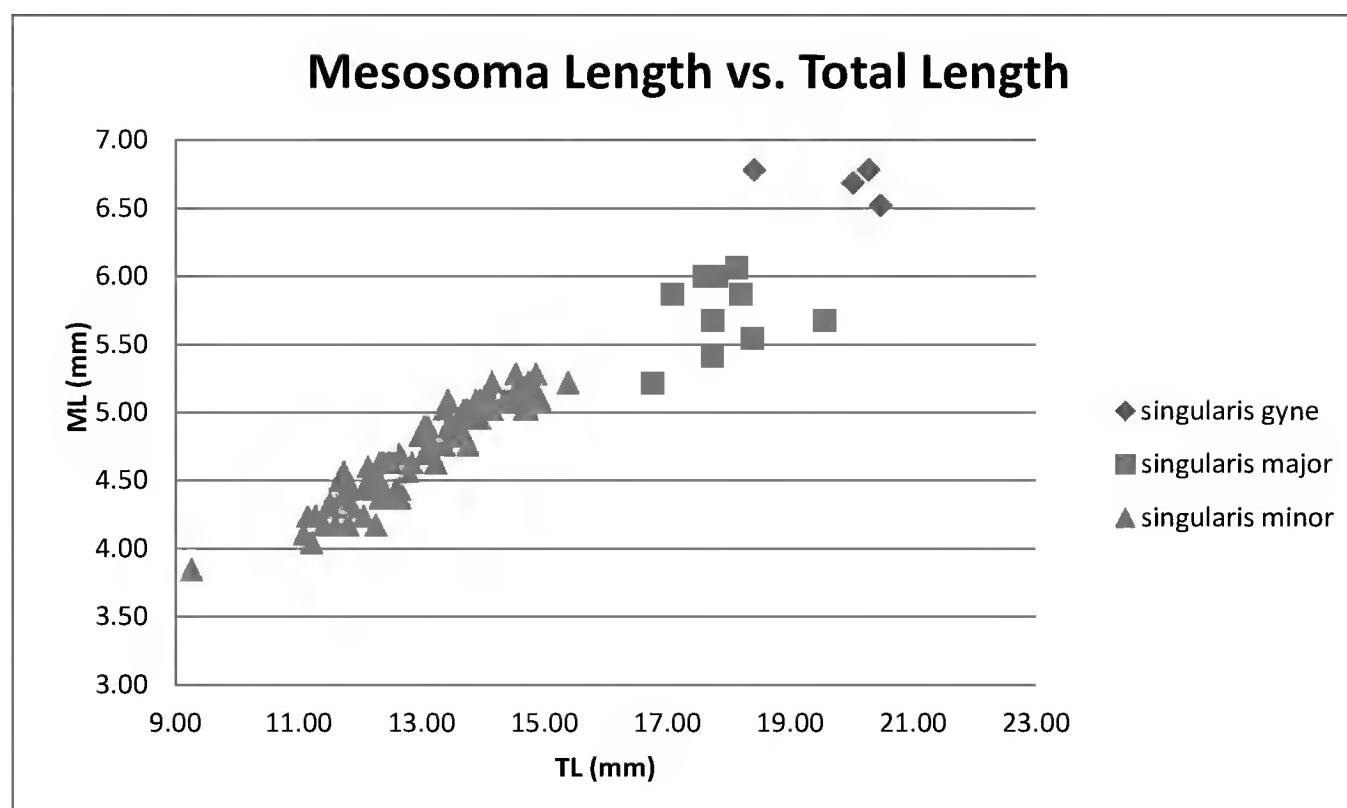


Figure 7. Distribution of mesosoma length (ML) in relation to total length (TL) in gynes, majors and minors of *Camponotus singularis*.

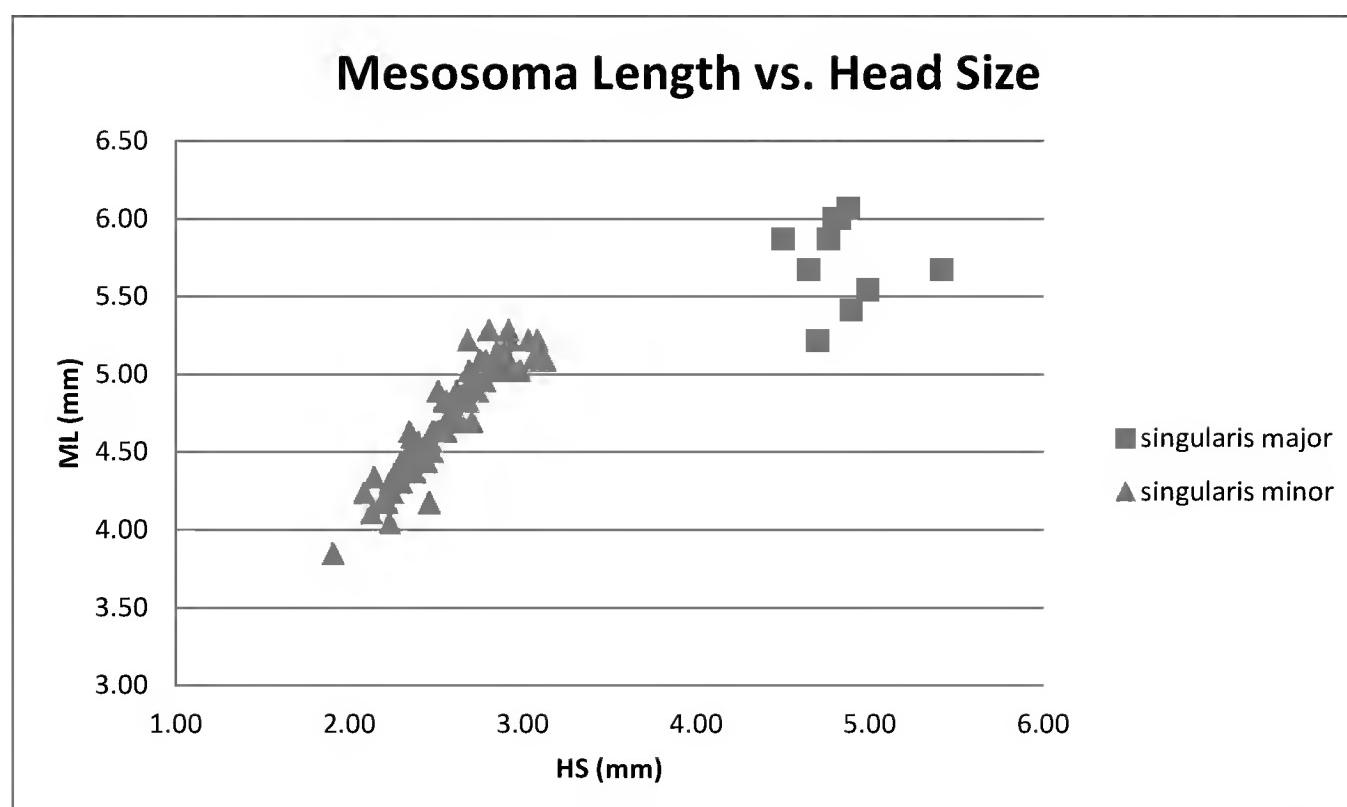


Figure 8. Distribution of mesosoma length (ML) in relation to head size (HS) in majors and minors of *Camponotus singularis*.

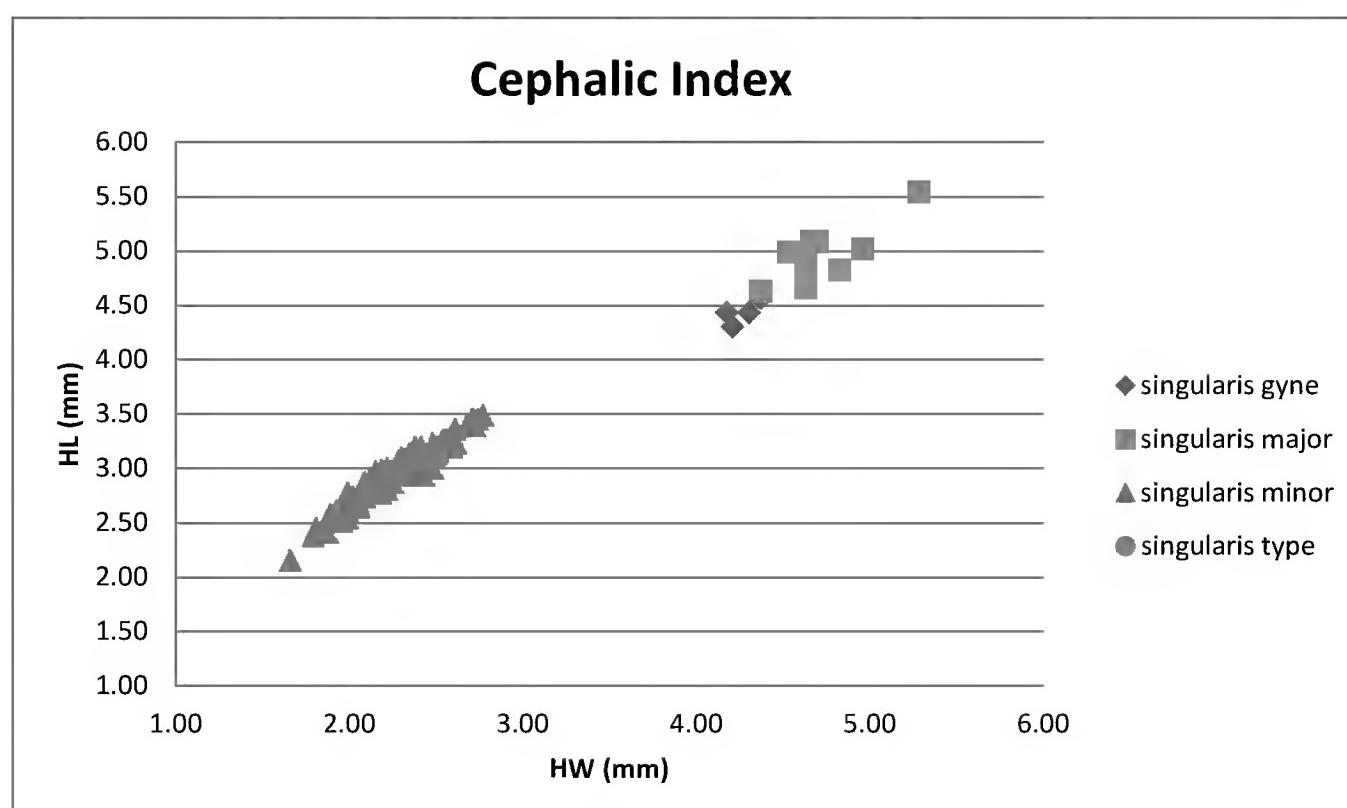


Figure 9. Distribution cephalic index (CI) in gynes, majors and minors of *Camponotus singularis*, holotype minor worker plotted separately.

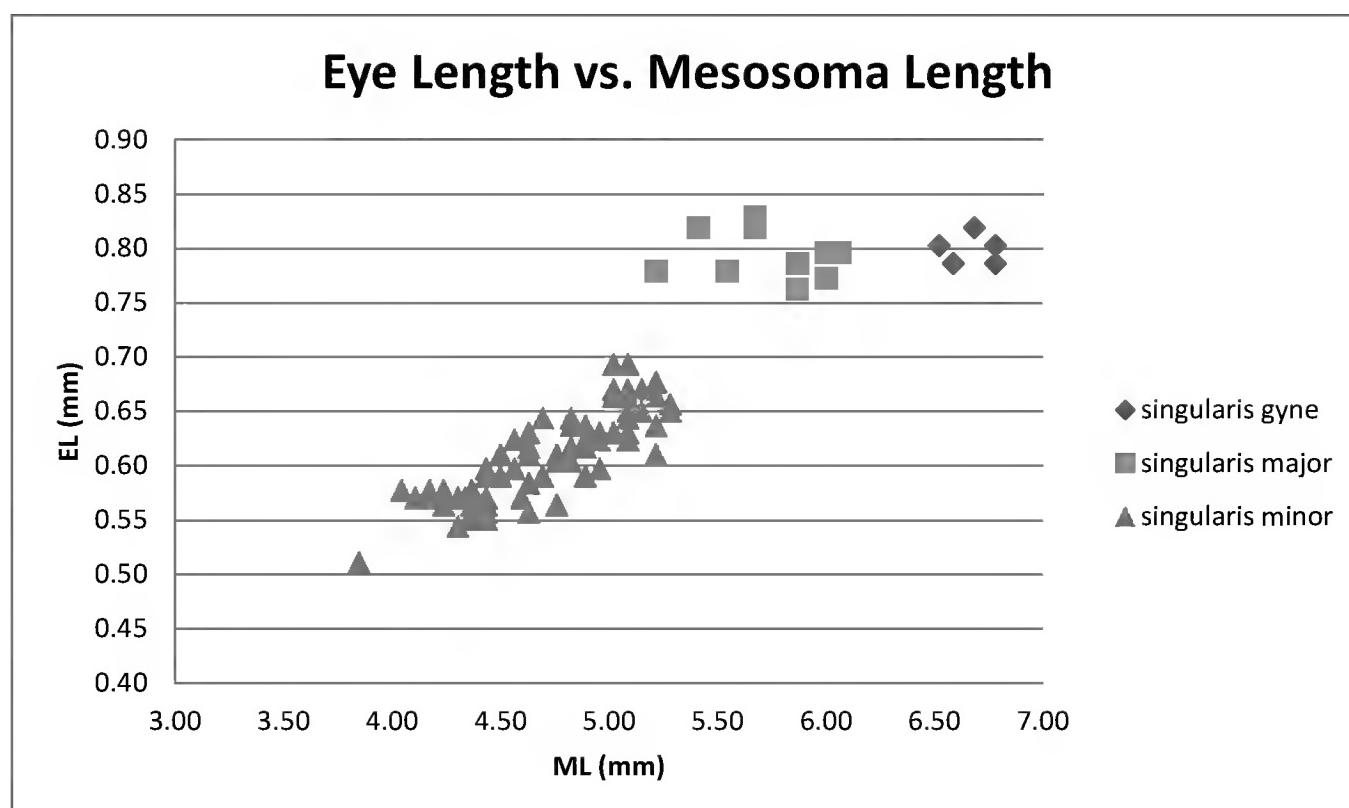


Figure 10. Distribution of eye length (EL) in relation to mesosoma length (ML) in gynes, majors and minors of *Camponotus singularis*.

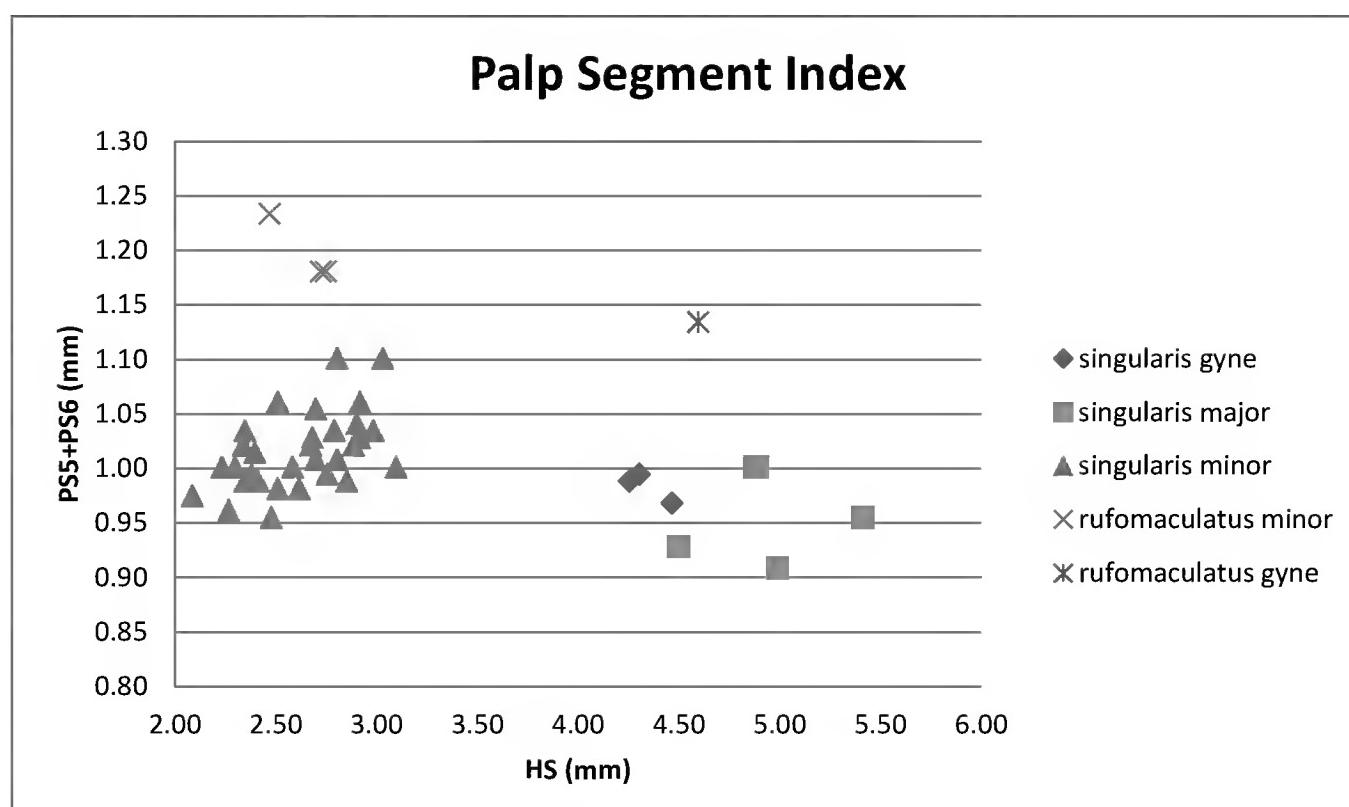


Figure 11. Distribution of maxillary palp segment index (PSI) in gynes, majors and minors of *Camponotus singularis*, as well as minors and gyne of var. *rufomaculatus*.

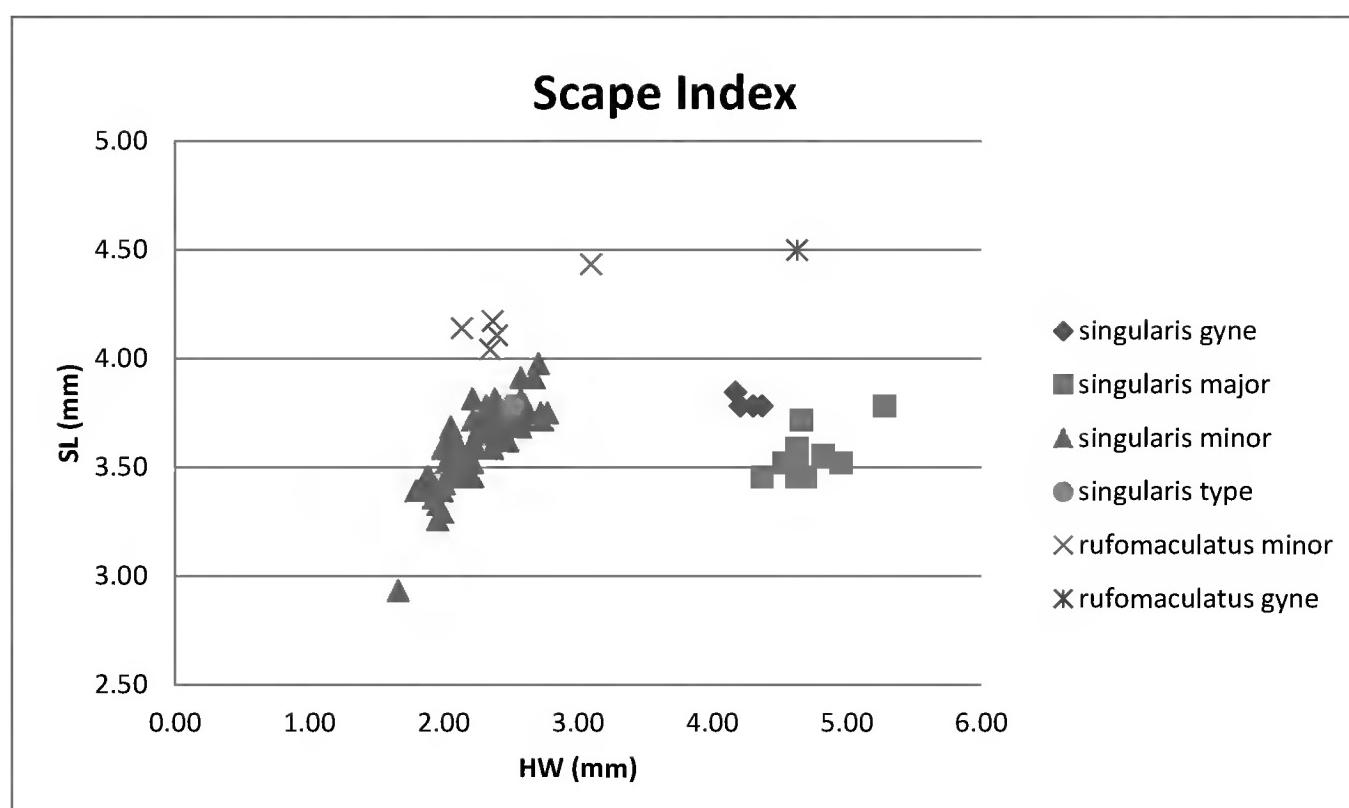


Figure 12. Distribution of scape index (SI) in gynes, majors and minors of *Camponotus singularis* (holotype minor worker plotted separately), as well as minors and gyne of var. *rufomaculatus*.

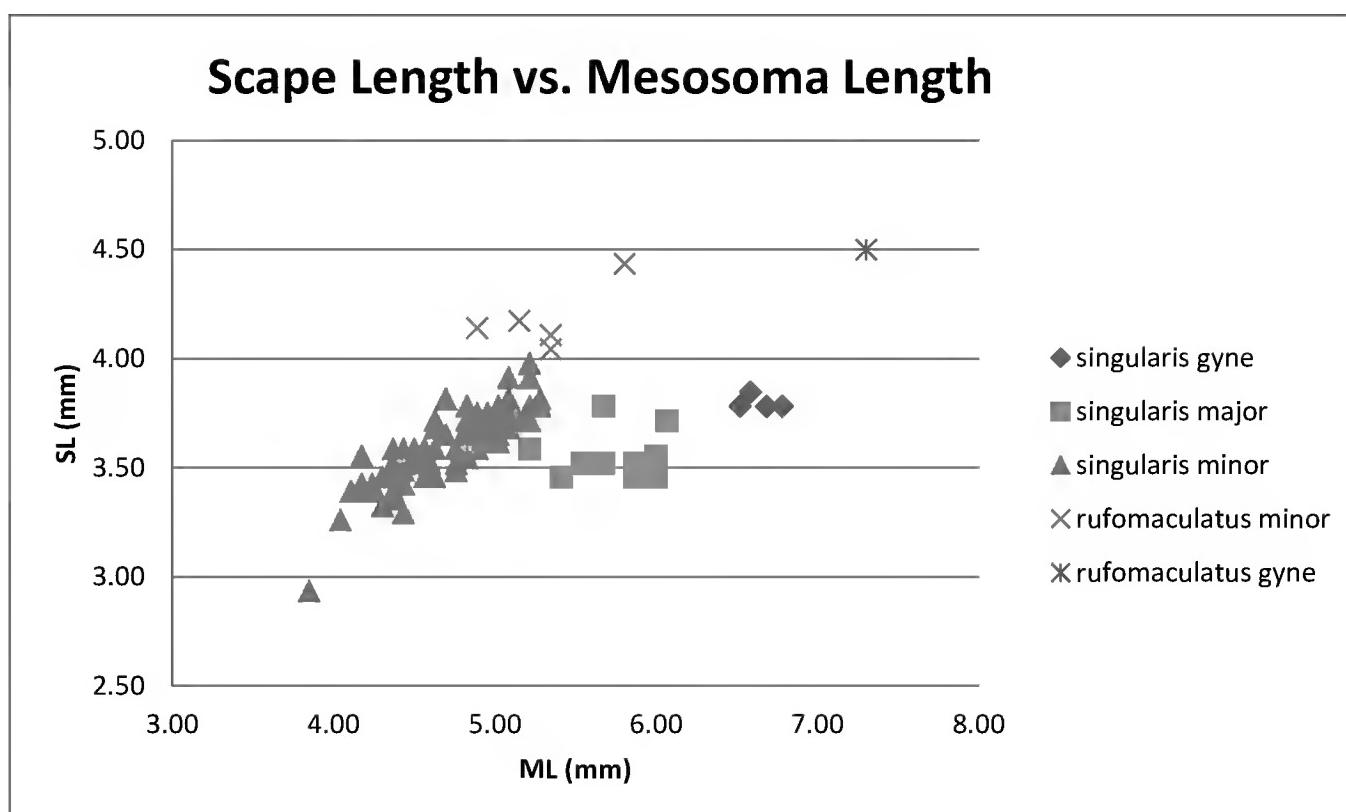


Figure 13. Distribution of scape length (SL) in relation to mesosoma length (ML) in gynes, majors and minors of *Camponotus singularis*, as well as minors and gyne of var. *rufomaculatus*.

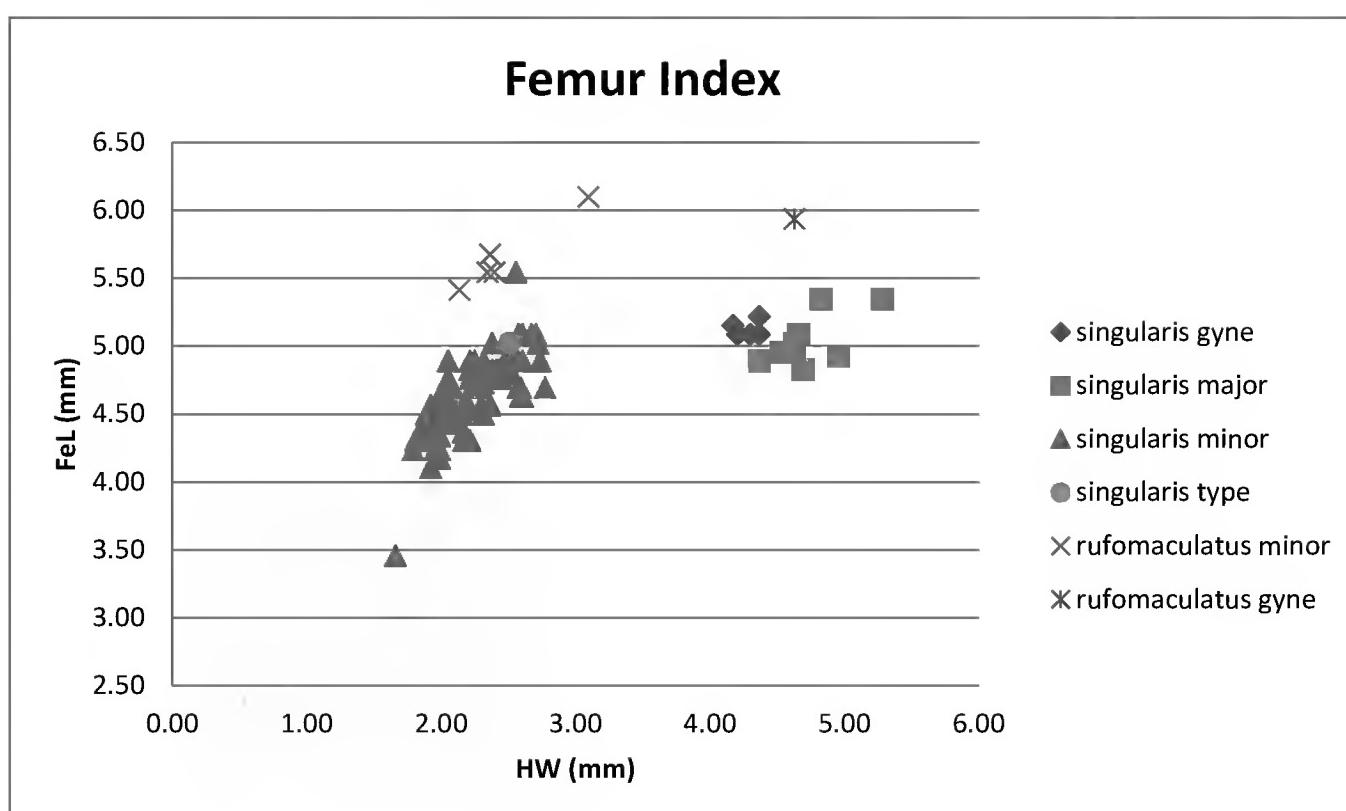


Figure 14. Distribution of femur index (FeI) in gynes, majors and minors of *Camponotus singularis* (holotype minor worker plotted separately), as well as minors and gyne of var. *rufomaculatus*.

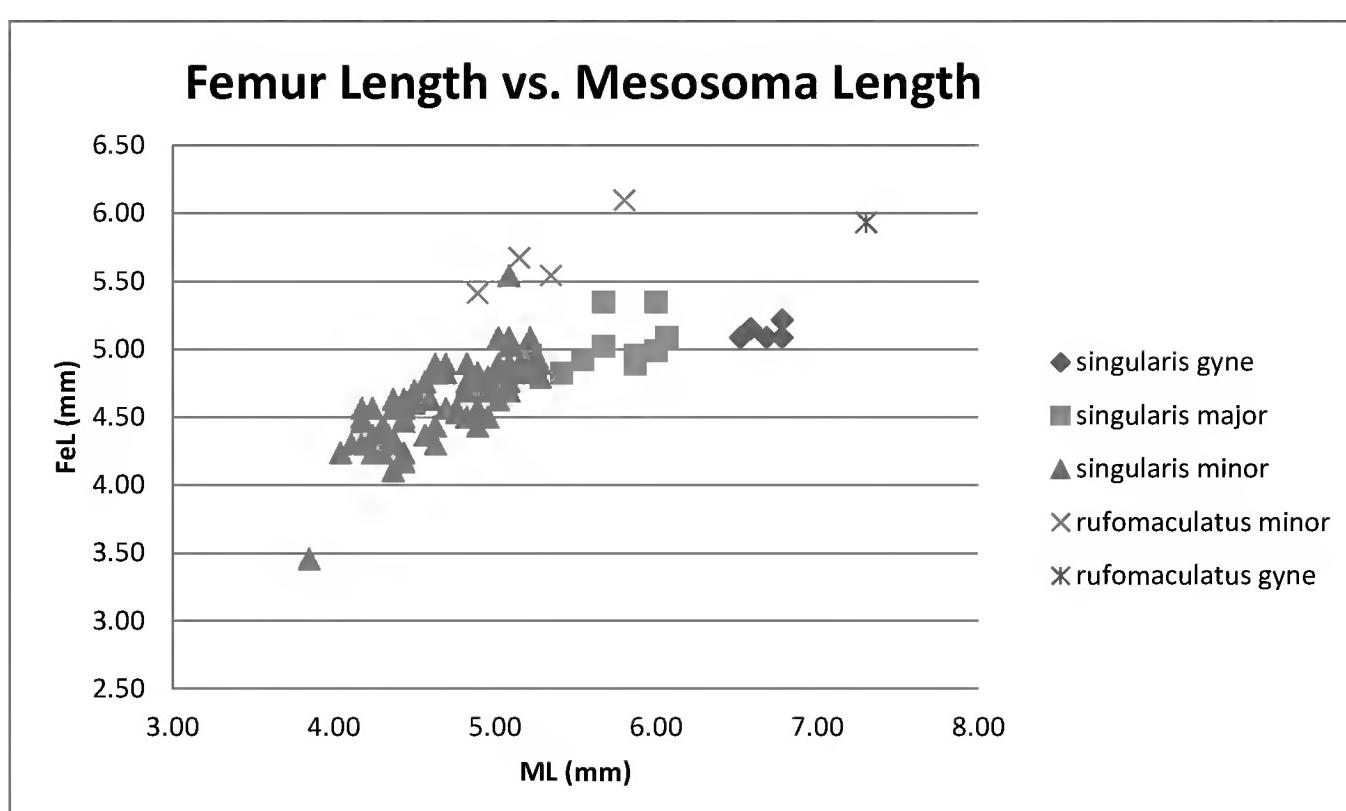


Figure 15. Distribution of femur length (FeL) in relation to mesosoma length (ML) in gynes, majors and minors of *Camponotus singularis*, as well as minors and gyne of var. *rufomaculatus*.

We used two measurements to describe body size, total length (TL) and mesosoma length (ML). Although traditionally used in myrmecology to facilitate rough comparisons of castes and species, total length strongly depends on the condition of the specimen (e.g., dilation or shrinking of the gaster from storage in alcohol or the drying process) so that TL can be relatively inaccurate. In *C. singularis* TL and ML are directly proportional in all female castes (Fig. 7). We therefore use ML as the main measurement for overall body size. There are two distinct subcastes of workers, minors and majors, which strongly differ in size range. Size variation is considerable in minors, whereas majors and gynes are more uniform in size (Fig. 7).

Head size and head shape:

Measurements: alate gynes (n = 5): HW 4.17–4.37; HL 4.30–4.63; HS 4.26–4.50; CI 94–98; major workers (n = 10): HW 4.37–5.28; HL 4.63–5.54; HS 4.50–5.41; CI 91–100; minor workers (n = 85): HW 1.66–2.77; HL 2.15–3.49; HS 1.91–3.13; CI 72–83.

HW and HL were measured. In relation to body size, head size (HS) is strongly disproportional in the two worker castes (Fig. 8). Major workers have a notably large head. The heads of gynes are also large, but on average less wide compared to major workers (Fig. 9).

The three castes differ considerably in head shape (Figs 1–3). In minor workers the ovate head is rounded posterior of the eyes, with a short, protruding collar; the narrow margin is dorsomedially depressed, and dorso-laterally slightly upcurved. In major workers the head is heart-shaped and posteriorly deeply concave. In gynes the head is slightly narrower than in majors and posteriorly almost straight. Furthermore, in both majors and gynes no collar or occipital margin is developed.

Eye size and eye position:

Measurements: alate gynes (n = 5): EL 0.79–0.82; EI 27–28; major workers (n = 10): EL 0.76–0.83; EI 23–27; minor workers (n = 85): EL 0.51–0.69; EI 36–46.

Eye size in minor workers is strongly correlated with body size (ML) (Fig. 10), and eyes appear smaller in majors since these workers have disproportionately large heads. In comparison to HW, the eyes of gynes are larger than those of major workers (EI 27–28 vs. 23–27).

In minor workers the eyes are dorsolaterally located, close to the lateral outline of the head in frontal view (Fig. 1). In contrast, the eyes of majors and gynes are shifted dorsally and placed approximately equidistant from the sides of the head and the frontal carinae (Figs 2, 3).

Ocelli:

Minor workers do not possess ocelli or other structures in their place. In one major worker from Myanmar we observed three reduced ocelli, whereas many other majors have small depressions or scars at these positions.

Clypeus shape:

The clypeus is similarly shaped in major and minor workers, whereas the medial protrusion is slightly longer in gynes (Figs 1–3). In major workers the lateral emarginations of the foremargin are wider than in minors to accommodate the thick bases of the mandibles.

Mandibles:

The mandibles of majors are much stouter than those of minors, especially in the basal half. The mandibles of gynes are of intermediate shape.

Maxillary palpi:

Measurements: alate gynes (n = 3): PS5 0.50–0.52; PS6 0.46–0.47; PSI 22–23; major workers (n = 5): PS5 0.49–0.54; PS6 0.42–0.48; PSI 18–21; minor workers (n = 32): PS5 0.52–0.60; PS6 0.42–0.50; PSI 32–47.

The maxillary palpi of minors are much longer in relation to HS than those of majors and gynes (PSI 18–23 in majors and gynes vs. 32–47 in minors; Fig. 11; see also Figs 1, 2). As palpi are very often obscured or damaged in mounted specimens, examination of this character was only possible in a small number of animals.

Antenna:

Measurements: alate gynes (n = 4): SL 3.78–3.85; SI 87–92; major workers (n = 10): SL 3.46–3.78; SI 71–80; minor workers (n = 83): SL 2.93–3.98; SI 135–189.

The antennae of majors and gynes are relatively shorter and thicker than those of minors. The scape index (SI) differs considerably (Fig. 12), but in relation to body size (ML), scape length is only slightly smaller in majors than in minors (Fig. 13).

Mesosoma shape:

The mesosoma of majors is slightly more robust (wider and higher) than that of minors, though no morphometric data were recorded except ML. Gynes always possess a well-developed flight apparatus, and their mesosoma morphology is strongly modified accordingly.

Leg length:

Measurements: alate gynes (n = 5): FeL 5.09–5.22; FeI 116–123; major workers (n = 10): FeL 4.83–5.35; FeI 101–114; minor workers (n = 85): FeL 4.46–5.45; FeI 169–238.

We measured the length of the hind femur (FeL) as an indicator for leg length. Whereas the femur index (FeI) is highly dissimilar in minors and majors (Fig. 14), majors have only slightly shortened legs compared to mesosoma length (Fig. 15). Gynes also possess shortened femora in comparison to minor workers, though the difference is not as pronounced as in majors (Fig. 14).

Petiole shape and petiole index:

Measurements: alate gynes (n = 5): PH 1.48–1.63; PL 1.04–1.17; NH 1.00–1.17; PI 134–144; major workers (n = 5): PH 1.13–1.48; PL 1.04–1.09 (4); NH 0.76–0.89 (4); PI 104–136 (4); minor workers (n = 49): PH 0.59–0.87 (38); PL 0.67–1.02 (35); NH 0.30–0.61 (46); PI 66–95 (31).

PI is highest in gynes, intermediate in majors and lowest in minors, reflecting the differences in dorsoventral height of the petiole and development of the petiolar node. While gynes and majors possess a petiole that is higher than long (PI > 100), with a well-developed node, the petiole of minors is dorsally rounded and longer than high (PI < 100). Due to the mounting method applied in some specimens, petiolar characters were partially obscured and therefore could not be measured in part of the material.

Gaster:

No evident differences were observed when comparing the gasters of minor and major workers. Due to the presence of reproductive organs, gynes possess a larger gaster relative to the rest of the body, but without apparent structural differences compared to the other castes.

Deviating characters of *Camponotus singularis* var. *rufomaculatus* from Borneo

The specimens from Borneo consistently differ from the rest of the examined material by the length of their appendages (maxillary palpi, antennae, and legs; Figs 11–15), as well as reddish colour of the dorsal mesosoma in some specimens, and darker setae on the head. Examination of photographs of the types of var. *rufomaculatus* (AntWeb: syntype major worker CASENT0903555, BMNH; syntype minor worker CASENT0903556, BMNH) suggests that this name is applicable to the Bornean population.

Maxillary palpi:

The examined gyne and minors of *C. s.* var. *rufomaculatus* possess relatively longer palpi than all the other examined specimens (PSI 43–50 in minors, 25 in gyne, see Fig. 11).

Antenna:

All examined *C. s.* var. *rufomaculatus* specimens differ from the rest of the material by considerably longer scapes relative to HW and ML (SI 143–194 in minors, 97 in gyne, see Figs 12, 13).

Leg length:

Camponotus singularis var. *rufomaculatus* differs from the typical form by relatively longer legs (FeI 197–253 in minors, 128 in gyne, see Figs 14, 15).

Discussion

Worker dimorphism and evolution of the major subcaste

The results of our morphometric analyses show that *C. singularis* possesses a true worker dimorphism sensu Wilson (1953) with distinct major and minor worker subcastes and without expression of intermediate morphology. As per the material represented in collections, majors have been observed to be much rarer compared to minors (85 minors and 10 majors examined). Although no complete nest series were available for analysis, the observed relatively low number of majors compared to minors agrees well with the results of previous studies on other Camponotini: Walker and Stamps (1986) as well as Hasegawa (1997) examined two species of *Colobopsis* and found optimal caste ratios of soldiers to lie at around 20% of the total nest-population.

Perhaps the most striking difference between the two worker subcastes is in the shape of the head, which is narrow and ovate with a well-developed collar in minors, but greatly enlarged, heart-shaped and without collar or margin in majors (Figs 1, 2). Though differing in the depth of the posterior concavity, the head-shape of majors is

strongly reminiscent of that of conspecific gynes (Fig. 3) with several major workers also possessing small ocelli or remnants thereof.

When comparing mesosomal architecture between castes, both major and minor workers possess a well-developed prothorax which is slightly enlarged in majors, whereas the mesothorax is greatly hypertrophied in gynes (Fig. 2). Keller et al. (2014) observed this morphological trade-off in multiple subfamilies of ants. They interpret a large prothorax as optimization for foraging and defence in workers, additionally providing attachments for muscles in large-headed majors, whereas the first mesosomal tergite is reduced in gynes to allow for the development of the flight apparatus. Additionally, majors and minors differ by the relative lengths of their appendages with major workers having consistently shortened legs, antennae and maxillary palpi when compared to conspecific minors (Figs 11–15). We could not find comparable data on Camponotini in the literature, but similar results were recently obtained in a study on *Colobopsis* sp. (Laciny et al., in prep., see below for details). In their study on leafcutter ants (*Atta colombica* Guérin-Méneville, 1844) and army ants (*Eciton hamatum* (Fabricius, 1782)), Feener et al. (1988) also found that legs became shorter with increasing body mass in workers of *Atta* and soldiers of *Eciton*. The authors attributed this result to the mechanics of foraging in the examined species. Shortened appendages relative to HS as well as to ML were also observed in the examined gynes of *C. singularis*, though to a slightly lesser extent than in majors. These observations of morphological similarities between majors and gynes may indicate the evolution of the developmental programme for major workers in this species by partial “recycling” of growth parameters for gyne-development (Molet et al. 2014). As elaborated in their 2014 study on *Cataglyphis bombycinus* (Roger, 1859), Molet et al. propose that the evolution of specialized castes may be facilitated by reusing and recombining parts of developmental programmes already established in pre-existing castes. The resulting phenotypes are therefore often characterized by a mosaic of novel and recycled traits that set them apart as a distinct caste. Our results clearly show that major workers of *C. singularis* are not simply isometrically scaled-up versions of minor workers, but differ from all other castes by shifts in morphological proportions resulting from differing growth rules; they may therefore be more accurately termed “soldiers” sensu Molet et al. (2012, 2014).

Comparison to other Camponotini

A recent study focusing on morphological variation in a species of the *Colobopsis cylindrica* (COCY) group (Laciny et al., in prep.) found considerable size-variation within the examined minor workers and relatively uniform sizes of major workers (phragmotic in *Colobopsis*) and gynes. This trend is in accordance with studies on other camponotines (e.g., Lee 1938, Busher et al. 1985, Espadaler et al. 1990) reporting wide size ranges in work-

ers that are often correlated with size-specific division of labour. A similar result was obtained in the present study: In *C. singularis* the largest minors surpass their smallest conspecifics by up to 50% regarding head width as well as mesosoma length, while majors and gynes show far less variability (Figs 7–9). Another parallel between the observations in COCY ants and *C. singularis* is the shortening of appendages relative to body size in the major worker subcaste: Majors of both groups possess shorter legs, antennae and maxillary palpi than conspecific minors. However, while in *C. singularis* this holds true for majors as well as gynes, in the COCY group only major workers have shortened appendages, whereas the proportions of gynes were more similar to those of minor workers. The caste-specific architecture of the mesosoma, with a prothorax that is enlarged in workers – particularly in large-headed majors – and reduced relative to the mesothorax in alate gynes, as observed in *C. singularis* and in species of the COCY group, conforms to the morphology of other studied ant species (Keller et al. 2014).

Polyethism and the role of soldiers

The results of this study show a clear worker dimorphism and a conspicuously broad size range of minors, which is apparent in intraspecific as well as intracolonial comparison. It is therefore a valid assumption that *C. singularis* colonies have evolved some form of polyethism or division of labour amongst their members. However, nothing is known about colony composition and task allocation in this species as of now. Studies on other formicine ants have yielded results that suggest a tendency towards division of labour even within the (minor) worker caste: Lee (1938) described such a trend in *Camponotus japonicus* var. *aterrimus* Emery, 1895, Busher et al. (1985) observed division of labour in *Camponotus sericeiventris* (Guérin-Méneville, 1838), and Higashi (1974) reported similar results for *Formica yessensis* Wheeler, 1913. In contrast, in the moderately polymorphic dolichoderine ant *Liometopum microcephalum* (Panzer, 1798) differences in task performance could not be detected (Petráková and Schlaghamerský 2014).

The high nutritional investment necessary for producing a distinct soldier subcaste suggests that these animals must serve a function greatly beneficial to colony survival and fitness (Tian and Zhou 2014). In many of the previously studied ant species the tasks of major workers or specialized soldiers do not only include nest defence, but also storage of food and liquid within their bodies: This was found to be true for the phragmotic major workers of *Colobopsis nipponica* (Wheeler, 1928) (Hasegawa 1993), large workers of the polymorphic *Camponotus foreli* Emery, 1881 (Espadaler et al. 1990) and the highly specialized soldiers of *Cataglyphis bombycinus* (Molet et al. 2014). Whether this is also the case in *C. singularis* still remains to be studied. In majors of *C. singularis* the greatly enlarged, heart-shaped head is correlated with the presence of strongly developed mandibular adductor muscles, most probably linked to a function in colony defence. The defensive be-

haviour of soldiers may also contribute to the development of shortened cephalic appendages (antennae, maxillary palpi), so as to reduce the danger of injury in combat. Mysore et al. (2009, 2010) reported major workers of *Camponotus compressus* (Fabricius, 1787) and *Camponotus sericeus* (Fabricius, 1798) to have shorter antennae with reduced sensilla and corresponding neural structures in comparison to conspecific minors. The authors link this to the majors' specialization in nest defence, which makes differentiation of chemical cues less essential than for foraging minor workers. Corresponding to the observed shortened antennae of majors, the situation may be similar in *C. singularis*. However, this can only be a tentative assumption at this point and requires further investigation.

Altogether the results obtained within this study and their comparison to trends observed in the COCY clade (Laciny et al., in prep.) and other previously studied species (e.g., Lee 1938, Wilson 1953, Espadaler et al. 1990, Mysore et al. 2009, 2010, Molet et al. 2012) lead us to propose *C. singularis* as a useful model to characterize major morphometric trends in camponotine caste dimorphism: a wide size range of minor workers, a major worker or soldier subcaste specialized for defence and characterized by an enlarged head and shortened appendages, and a mosaic of novel, gyne-like, and worker-like traits expressed in such specialized phenotypes.

Differing characters of var. *rufomaculatus*

Examined specimens from Borneo clearly differ from specimens from other localities by proportions of appendages, colour pattern and setae. Donisthorpe (1941) originally described var. *rufomaculatus* as a colour variation of *Camponotus singularis*. New data suggest that this name might be applied to a distinct species. Taxonomic implications and details on this issue will be the subject of a separate publication after having examined the types of var. *rufomaculatus* (Zettel et al. in prep.). Faunistic data suggest that this form may be endemic to the island of Borneo, as no matching specimens from other proveniences have been reported so far.

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Supplementary material 1

Table S1: Measurements (mm) of all examined specimens of *Camponotus singularis* (n = 100) and *C. s. var. rufomaculatus* (n = 6).

Authors: Alice Laciny, Herbert Zettel, Irina Druzhinina

Data type: specimens data

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Review of the world species of *Exoryza* (Hymenoptera, Braconidae, Microgastrinae), with description of five new species

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Abstract

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The world species of the genus *Exoryza* (Hymenoptera, Braconidae, Microgastrinae) are revised. Ten species are recognized, including five new, authored by Fernandez-Triana: *mariabustosae*, *richardashleyi*, *ritaashleyae*, *rosamatarritae* and *yeimycedenoae*. The species *Dolichogenidea oryzae* Walker, 1994 is considered as related to *Exoryza* – although is not formally transferred to that genus. A dichotomous key to all species, descriptions and illustrations are provided. The only region where the genus is not yet recorded is Australasia, but this may be a collecting artifact. Host caterpillars (Lepidoptera) include species within Choreutidae, Depressariidae, Gelechiidae, and Pyraloidea – all but Pyraloidea are new host records. The status of *Exoryza* is questioned (it may only represent a species-group within the genus *Dolichogenidea*) but it is retained as a valid genus until a comprehensive phylogenetic study of Microgastrinae is available.

Introduction

The braconid subfamily Microgastrinae contains more than 60 genera (Yu et al. 2012), many of them lacking comprehensive revisions and keys to their species. *Exoryza* is a rarely collected genus (Mason 1981, Valerio et al. 2004), and it is poorly represented in collections. It was described by Mason (1981) to include two species of Apantelini (*sensu* Mason 1981) with broad and heavily sculptured metasomal tergites 1–2, and a coarsely rugose and areolate propodeum. Three other species have since been described (Song and Chen 2003, Valerio et al. 2004, Rousse and Gupta 2013), expanding the known distribution of the genus to all continents but Australia.

Here we review *Exoryza*, as it occurs in Area de Conservación Guanacaste (ACG), northwestern Costa Rica (Janzen et al. 2009, Janzen and Hallwachs 2011), as part

of comprehensive studies of ACG Microgastrinae (e.g., Fernandez-Triana et al. 2014). Five new species are described, and a key to the known *Exoryza* of the world is provided.

Methods

Most of the specimens studied were Malaise-trapped or reared in ACG, and a few additional specimens were available in the Canadian National Collection of Insects (CNC) in Ottawa, Canada. Five species of *Exoryza* had been described previously; we were able to examine the holotypes of *E. minnesota* and *E. monocavus*, but the original descriptions and illustrations of the rest were sufficiently detailed to allow description of the new species with confidence.

The following institution acronyms are used:

BMNH	The Natural History Museum, London, United Kingdom
FAFU	Fujian Agriculture and Forestry University, Fujian, China
INBio	Instituto Nacional de Biodiversidad, San José, Costa Rica
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NMNH	National Museum of Natural History, Washington DC, United States.

Morphological terms, measurements of structures, and body ratios are mostly as used by Mason (1981), Huber and Sharkey (1993), Whitfield (1997), Karlsson and Ronquist (2012), and Fernández-Triana et al. (2014). Mediotergites 1, 2, etc., are abbreviated as T1, T2, etc; ocular ocellar line as OOL, and posterior ocellar line as POL. The diagnostic descriptions include characters that are commonly used in describing Microgastrinae (e.g., body measurements such as length of body, fore wing and ovipositor sheath, hind wing vannal lobe shape and fringe, and color of particular body areas).

The dichotomous key and descriptions of the new species are based on the study of all available female specimens, to assess intraspecific variation. Body measurements shown are mostly from the holotype specimens. Whenever possible, information on additional female specimens was also included, between parentheses after the holotype data; the voucher codes of those specimens are provided under ‘Paratypes’ in the corresponding description of each species. Males were not studied morphologically, as most species can only be readily identified by association with females via rearing or molecular data.

Photos were taken with a Keyence VHX-1000 Digital Microscope, using a lens with a range of 13–130×. Multiple images through the focal plane were taken of a structure and these were combined to produce a single in-focus image, using the software associated with the Keyence System.

Together with morphological studies, we also analyzed DNA barcodes (the 5' region of the cytochrome c oxidase I (CO1) gene, Hebert et al. 2003) whenever available. DNA barcodes were obtained using DNA extracts prepared from single legs using a glass fibre protocol (Ivanova et al. 2006). Briefly, total genomic DNA was re-suspended in 30 µl of dH₂O, and a 658-bp region near the 5' terminus of the CO1 gene was amplified using standard primers (LepF1–LepR1) following established protocols (Smith et al. 2006, 2007, 2008). If the initial 658 bp amplification was unsuccessful, smaller sequences were generated using internal primers. If each amplification was successful, a composite sequence was generated. However in cases where only one read amplified, this shorter sequence was used. A neighbor-joining (NJ) tree

based on Kimura 2-parameter to visually demonstrate the variation present within and between each species in the DNA barcode locus is presented in Figure 40. All information for the sequences (including GenBank accessions) associated with each individual specimen can be retrieved from the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert 2007) using the persistent DOI dx.doi.org/10.5883/DS-ASEXORYZ [requested April 15, 2016 but not yet active].

The new ACG species described below received patronyms honoring the teachers and supporters of a biodiversity conservation event and school child nature awareness competition, conducted by the Programa de Educación Biológica (PEB) of ACG in the last half of 2015 (Kazmier 2015).

Results

Diagnosis and status of *Exoryza*

Diagnosis. Heavily sculptured and broad T1 and T2 (usually with strong longitudinal striation); T2 rectangular or nearly so, as long as or longer than T3 (Figs 5, 12, 18, 24, 31, 38); fore wing without areolet; vannal lobe straight to concave, uniformly fringed by setae (Figs 4, 11, 17, 35); propodeum sculptured and with areola (but sometimes areola obscured by other sculpture) (Figs 4, 11, 17, 18, 23, 24, 30, 37). The uniformly setose vannal lobe separates *Exoryza* from *Apanteles*, while the sculpture of T1 and T2 distinguishes *Exoryza* from *Dolichogenidea* (but see below).

The status of *Exoryza* as a valid genus has been questioned by many authors (e.g., Valerio et al. 2004, Rousse and Gupta 2013, Fernandez-Triana et al. 2014). Mason (1981) characterized *Exoryza* as having T1 and T2 heavily sculptured, and propodeum coarsely rugose (with areola present but obscured by propodeum sculpture). The distinction between it and *Dolichogenidea* is particularly difficult (e.g., Fernandez-Triana et al. 2014), since many species of *Dolichogenidea* have a sculptured propodeum (with or without areola), and T1 is occasionally sculptured (although not as strongly as in *Exoryza*). T2 is also more or less broadly trapezoidal in shape in *Exoryza*, without the more or less sinuate hind margin many *Dolichogenidea* species have. All known sequences (DNA barcodes) of *Exoryza* cluster together in a NJ tree containing more than 50 genera and 17,518 sequences of world species of Microgastrinae (see Appendix S2 in Smith et al. 2013, page 41, sequences 4019–4041); but they are within a larger cluster containing *Dolichogenidea* (and a few specimens of *Parapanteles* and *Apanteles* which were most likely misidentified and are actually *Dolichogenidea*). With no recent, comprehensive phylogenetic study of Microgastrinae available, we consider it best to maintain *Exoryza* as a valid genus for the time being.

Diversity and host data

Five species of *Exoryza* were previously known (Mason 1981, Song and Chen 2003, Valerio et al. 2004, Rousse and Gupta 2013), and five new species are described below for a total of 10 species worldwide. *Dolichogenidea oryzae* Walker, 1994 could probably be included within *Exoryza* as well –based on the examined specimens (including holotype), host data (*Chilo* spp.) and distribution (West Africa), that species fits well within the generic concept used in the present paper. However, we have refrained from transferring *D. oryzae* to *Exoryza* due to the possibility that in the future *Exoryza* becomes a synonym of *Dolichogenidea* –see comments in previous paragraphs. But we include *D. oryzae* in the dichotomous key for *Exoryza* species provided below.

Exoryza seems to be almost cosmopolitan, with one species recorded from the Nearctic, six Neotropical, one Afrotropical, one Oriental, and one species found in both

the Oriental and Eastern Palaearctic regions (Table 1). So far the only region where the genus has not been recorded is Australasia, but this may be a collecting artifact. We anticipate that additional species will be found as more collecting and study of world collections advances.

Only one of the five previously described species, *E. schoenobii* (Wilkinson), had associated host data. It was reared from five species of Lepidoptera within four genera of Pyraloidea (Yu et al. 2012). That wasp species has been rather extensively studied as a biocontrol agent of stem-boring Lepidoptera in rice fields in Asia (see compilation of references in Yu et al. 2012). Here we report additional hosts species for *Exoryza*, all based on rearing from small leaf-rolling and leaf-silking caterpillars in ACG (Janzen et al. 2009): Choreutidae (*Brenthia Janzen05*), several species of Gelechiidae (subfamily Dichomeridinae, with interim names ‘gelJanzen01 Janzen16’, ‘gelJanzen01 Janzen319’, ‘gelJanzen01 Janzen349’), and Depressariidae (*Stenoma Phillips543*).

Table 1. World species of *Exoryza*. Geographical distribution and associated host data from Yu et al. (2012) and the present paper. ACG- Area de Conservación Guanacaste; AFR- Afrotropical; NEA- Nearctic; NEO- Neotropical; OTL- Oriental; PAL- Palaearctic. (*)- New country record. The species *Dolichogenidea oryzae* Walker, 1994 is also included (see text for explanation about that species).

<i>Exoryza</i> species	Geographical distribution	Host	Host Plant
<i>D. oryzae</i> Walker, 1994	AFR (Gambia (*), Ivory Coast, Niger, Senegal)	Pyraloidea: <i>Chilo diffusilineus</i> (de Joannis), <i>Chilo zacconius</i> Bleszynski, 1970	<i>Oryza sativae</i> (Poaceae)
<i>E. mariabustosae</i> Fernandez-Triana	NEO (Costa Rica: ACG)	Gelechiidae: ‘gelJanzen01 Janzen319’	<i>Sloanea faginea</i> (Elaeocarpaceae)
<i>E. minnesota</i> Mason, 1981	NEA (Canada: Ontario; US: Minnesota)	Unknown	Unknown
<i>E. monocavus</i> Valerio & Whitfield, 2004	NEO (Costa Rica: Punta Arenas)	Unknown	Unknown
<i>E. reticarina</i> Song & Chen 2003	OTL (China: Yunan)	Unknown	Unknown
<i>E. richardashleyi</i> Fernandez-Triana	NEO (Costa Rica: ACG)	Gelechiidae: ‘gelJanzen01 Janzen349’	Unknown
<i>E. ritaashleyae</i> Fernandez-Triana	NEO (Costa Rica: ACG)	Unknown	Unknown
<i>E. rosamatarritae</i> Fernandez-Triana	NEO (Costa Rica: ACG)	Choreutidae: ‘ <i>Brenthia Janzen05</i> ’; Depressariidae: ‘ <i>Stenoma Phillips543</i> ’; Gelechiidae: ‘gelJanzen01 Janzen16’	<i>Desmopsis schippii</i> (Annonaceae), <i>Pterocarpus officinalis</i> (Fabaceae), <i>Pachira aquatica</i> (Malvaceae)
<i>E. schoenobii</i> (Wilkinson, 1932)	OTL/PAL (Bangladesh; China: Fujian, Guangdong, Guangxi, Guizhou, Hainan Island, Hubei, Hunan, Jiangsu, Jiangxi, Sichuan, Taiwan, Yunnan, Zhejiang; India; Malaysia, Philippines; Sri Lanka; Vietnam)	Pyraloidea: <i>Chilo polychrysus</i> (Meyrick, 1932); <i>C. suppressalis</i> (Walker, 1863); <i>Glaucoccharis reniella</i> Wang & Sung, 1988; <i>Schoenobius bipunctifer</i> Strand, 1918, <i>Scirpophaga incertulas</i> (Walker, 1863)	Unknown
<i>E. safranum</i> Rousse & Gupta 2013	AFR (Réunion)	Unknown	Unknown
<i>E. yeimycedenoae</i> Fernandez-Triana	NEO (Costa Rica: ACG)	Unknown	Unknown

Key to known species of *Exoryza* and *Dolichogenidea oryzae* (see text for explanation about inclusion of the *Dolichogenidea* species).

- 1 Basal tergites reddish-yellow, metasoma mostly yellow; ovipositor sheaths 0.7 x as long as metatibia [China] *Exoryza reticarina* Song & Chen, 2003
- Basal tergites black, metasoma mostly dark brown to black (Figs 5, 12, 18, 24, 31, 38); ovipositor sheaths usually as long as or longer than metatibia length 2
- 2(1) Metacoxa and metafemur entirely black; ovipositor sheaths almost twice as long as metatibia [Réunion island] *Exoryza safranum* Rousse & Gupta, 2013
- Metacoxa and metafemur entirely to partially yellow; ovipositor sheaths much shorter (0.7–1.5 x as long as metatibia) .. 3
- 3(2) T1 strongly broadening towards posterior margin (Figs 3, 5), its length 0.8–1.0 x its width at posterior margin, and its width at anterior margin 0.5–0.7 x its width at posterior margin; propodeum areola obscured by surrounding heavy sculpture (Figs 4, 5); metapleuron entirely sculptured [Old World tropics] 4
- T1 less strongly broadening towards posterior margin (Figs 12, 18, 24, 31, 38), its length at least 1.1 x its width at posterior margin (usually more) and its width at anterior margin 0.8–0.9 x its width at posterior margin; propodeum areola clearly marked by carinae (Figs 11, 17, 18, 23, 24, 30); metapleuron mostly smooth [New World] 5
- 4(3) Mesopleuron mostly smooth (Fig. 6); metafemur length 2.9 x metatibia length (Fig. 6); malar line 0.9 x mandible width (Fig. 1); ovipositor sheaths 0.7 x metatibia length [Afrotropics: Gambia, Ivory Coast, Niger, Senegal] *Dolichogenidea oryzae* Walker, 1994
- Mesopleuron entirely sculptured; metafemur length 3.1 x metatibia length; malar line 0.5 x mandible width; ovipositor sheaths as long as metatibia length [Oriental: Bangladesh, China, India, Malaysia, Philippines, Sri Lanka, Vietnam].... *Exoryza schoenobii* (Wilkinson, 1932)
- 5(3) T1 barrel-shaped, with lateral margins convex; metapleuron with medial pit present but not conspicuously deep or evident [Nearctic: USA and Canada] *Exoryza minnesota* Mason, 1981
- T1 parallel-sided to slightly widening towards posterior margin, with lateral margins straight (Figs 12, 18, 24, 31, 38); metapleuron with a conspicuously deep central pit [Neotropics: Costa Rica] 6
- 6(5) Body length 2.3–2.5 mm; metatibia dark brown to black on posterior 0.5–0.7 (Figs 13, 32)..... 7
- Body length 3.1–3.8 mm; metatibia dark brown to black on posterior 0.1–0.2 (Figs 19, 25, 39) 9
- 7(6) Flagellomere 16 length 2.5 x flagellomere 15 length; ocular ocellar line 1.4 x posterior ocellar line; metafemur length 3.4 x its width; metatibia dark brown to black on posterior 0.5 [Costa Rica: Puntarenas, at 1,000–1,035 m]..... *Exoryza monocavus* Valerio & Whitfield, 2004
- Flagellomere 16 length 1.2 x flagellomere 15 length; ocular ocellar line 1.0–1.1 x posterior ocellar line; metafemur length 3.6–3.8 x its width; metatibia dark brown to black on posterior 0.6–0.7 [Costa Rica, ACG, mostly collected at 500–600m] 8
- 8(7) T3 entirely smooth (Fig. 12); T1 and T2 mostly with longitudinally striated sculpture (Fig. 12); tarsal claws of hind legs with single spine-like basally *Exoryza mariabustosae* Fernandez-Triana, sp. n.
- T3 sculptured on anterior 0.2–0.5 (but mostly centrally) (Fig. 31); T1 and T2 mostly with reticulate sculpture (Fig. 31); tarsal claws of hind legs simple *Exoryza rosamatarritae* Fernandez-Triana, sp. n.
- 9(6) Pterostigma with pale yellow spot on proximal 0.5 (Fig. 16); smaller species (body length 3.1 mm and fore wing length 3.4 mm); thinner metafemur (4.1 x as long as maximum width) (Fig. 19)..... *Exoryza richardashleyi* Fernandez-Triana, sp. n.
- Pterostigma mostly brown, at most with small pale spot on proximal 0.1–0.2 (Figs 22, 36); larger species (body length 3.3–3.8 mm and fore wing length 3.5–4.1 mm); thicker metafemur (3.6–3.8 x as long as maximum width) (Figs 25, 39) 10
- 10(9) Metatibial spurs with brown tips; flagellomere 2 length 2.1 x flagellomere 14 length *Exoryza yeimycedenoae* Fernandez-Triana, sp. n.
- Metatibial spurs entirely yellow; flagellomere 2 length 2.5 x flagellomere 14 length..... *Exoryza ritaashleyae* Fernandez-Triana, sp. n.

Taxonomic treatment of species

***Dolichogenidea oryzae* Walker, 1994**

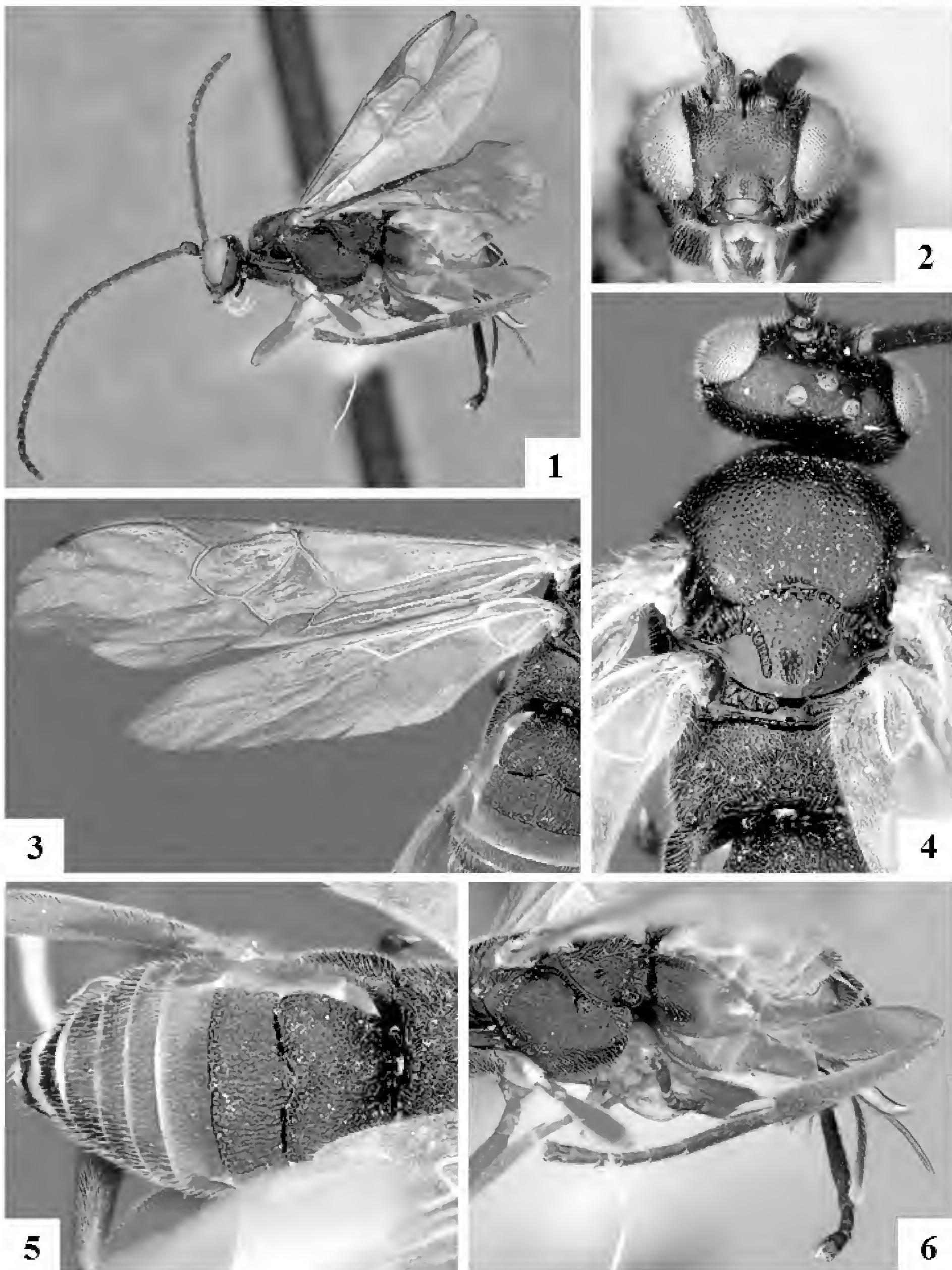
Figs 1–6

Dolichogenidea oryzae Walker, 1994: 426. Original description.

Holotype. Female, BMNH (examined). SENEGAL: Ziguinchor, Djibelor, 5.ix.1981 (J. Etienne leg.), Braconidae ectoparasite de *Chilo sur Riz*, CIE A17916.

Other specimens examined. 1 #F (CNC), Republic of the Gambia, Bakan, 19.i.1978, coll. L. Huggert. DNA voucher code: CNCHYM 01202.

Diagnostic description. Body color. Head (except for clypeus and mandibles), mesosoma and T1–T2 black,



Figures 1–6. *Dolichogenidea oryzae*.

remaining mediotergites brown; laterotergites, sternites and hypopygium yellow; antennal flagellomeres brown; tegula and wing base yellow; pterostigma mostly brown (with small pale spot on proximal 0.1); legs mostly yellow-orange except for metacoxa (black on proximal 0.6, yellow-orange on distal 0.4), metafemur (distal 0.2 dorsally brown), metatibia (distal 0.3 brown), and metatarsus (brown). **Body ratios.** Flagellomere 2 length/width: 3.2 x. Flagellomere 14 length/width: 2.0 x. Malar line/mandible width: 0.9 x. Metafemur length/width: 2.9 x. Metatibial inner/outer spur length: 1.2 x. T1 length/width at posterior margin: 0.7 x. T2 length/width at posterior margin: 0.4 x. Ovipositor sheaths length/metatibia length: 0.7 x. **Body measurements (all in mm).** Body length: 3.2. Fore wing length: 3.4. Flagellomere 2 length/width: 0.26/0.08. Flagellomere 14 length/width: 0.13/0.065. Flagellomeres 1/2/3/14/15/16 length: 0.27/0.26/0.26/0.13/0.12/0.16. OOL: 0.15. POL: 0.13. Diameter of posterior ocellus: 0.07. Malar line/mandible width: 0.09/0.10. Metafemur length/width: 0.75/0.26. Metatibia length: 1.08. First segment of metatarsus length: 0.51. Metatibial inner/outer spur length: 0.28/0.23. T1 length/width at anterior margin/width at posterior margin: 0.46/0.36/0.65. T2 length/width at posterior margin: 0.30/0.71. T3 length: 0.21. Ovipositor sheaths length: 0.75.

Biology. Reared from Pyraloidea (*Chilo diffusilineus* (de Joannis), *Chilo zacconius* Bleszynski, 1970) (Walker 1994).

Distribution. Gambia, Ivory Coast, Niger, Senegal.

Notes. All available evidence (morphology, biology) strongly suggests this species belongs to *Exoryza*. But we have not transferred the species to that genus due to the possibility that *Exoryza* is synonymized under *Dolichogenidea* in the future (see further discussion on the topic above). The diagnostic description provided above, as well as the pictures of the species were based on the female specimen deposited in the CNC. For more details, the original description of the species (Walker 1994) should also be consulted.

Exoryza mariabustosae Fernandez-Triana, sp. n.

<http://zoobank.org/8C75D0A4-4EF7-4C82-8589-162345CD0428>

Figs 7–13

Holotype. Female, CNC. COSTA RICA: Guanacaste, ACG, Sector Pitilla, Sendero Cuestona, 640m, 10.99455, -85.41461, 5.ix.2011, coll. Manuel Rios. DNA voucher code: DHJPAR0048181.

Paratypes. 4 #M (CNC, NMNH). Costa Rica, Alajuela, ACG. DNA voucher codes: DHJPAR0051074, DHJPAR0051184, DHJPAR0052269, DHJPAR0052281.

Diagnostic description. Body color. Head (except for clypeus and mandibles), mesosoma and metasoma (dorsally) dark brown to black; laterotergites, sternites and hypopygium partially yellow, partially dark

brown; antennal flagellomeres dark brown; tegula and wing base white-yellow; pterostigma mostly brown (with small pale spot on proximal 0.1); legs mostly white-yellow except for metacoxa (black on proximal 0.7, white-yellow on distal 0.3), metafemur (distal 0.1 dorsally brown), metatibia (distal 0.7 dark brown), and metatarsus (dark brown). **Body ratios.** Flagellomere 2 length/width: 3.1 x. Flagellomere 14 length/width: 1.3 x. Malar line/mandible width: 1.1 x. Metafemur length/width: 3.6 x. Metatibial inner/outer spur length: 1.2 x. T1 length/width at posterior margin: 1.2 x. T2 length/width at posterior margin: 0.4 x. Ovipositor sheaths length/metatibia length: 0.9 x. **Body measurements (all in mm).** Body length: 2.5. Fore wing length: 2.7. Flagellomere 2 length/width: 0.23/0.075. Flagellomere 14 length/width: 0.09/0.07. Flagellomeres 1/2/3/14/15/16 length: 0.22/0.23/0.21/0.09/0.09/0.11. OOL: 0.12. POL: 0.11. Diameter of posterior ocellus: 0.065. Malar line/mandible width: 0.08/0.07. Metafemur length/width: 0.72/0.20. Metatibia length: 0.82. First segment of metatarsus length: 0.41. Metatibial inner/outer spur length: 0.19/0.16. T1 length/width at anterior margin/width at posterior margin: 0.40/0.29/0.33. T2 length/width at posterior margin: 0.18/0.46. T3 length: 0.14. Ovipositor sheaths length: 0.70.

Male. As female but metacoxa and metatibia entirely dark brown to black, and T1–T2 narrower and smaller.

Biology. Reared from Gelechiidae (an undetermined species with interim name ‘gelJanzen01 Janzen319’).

Distribution. Costa Rica, Alajuela and Guanacaste provinces, ACG (Sectors Pitilla, San Cristobal and Rincon Rain Forest), between 527–980m.

Etymology. Named in honor of María Margarita Bustos González for her enthusiasm in teaching her La Garita Vieja students to understand and protect the wild nature that occurs in her homeland.

Exoryza minnesota Mason, 1981

Exoryza minnesota Mason, 1981: 40. Original description.

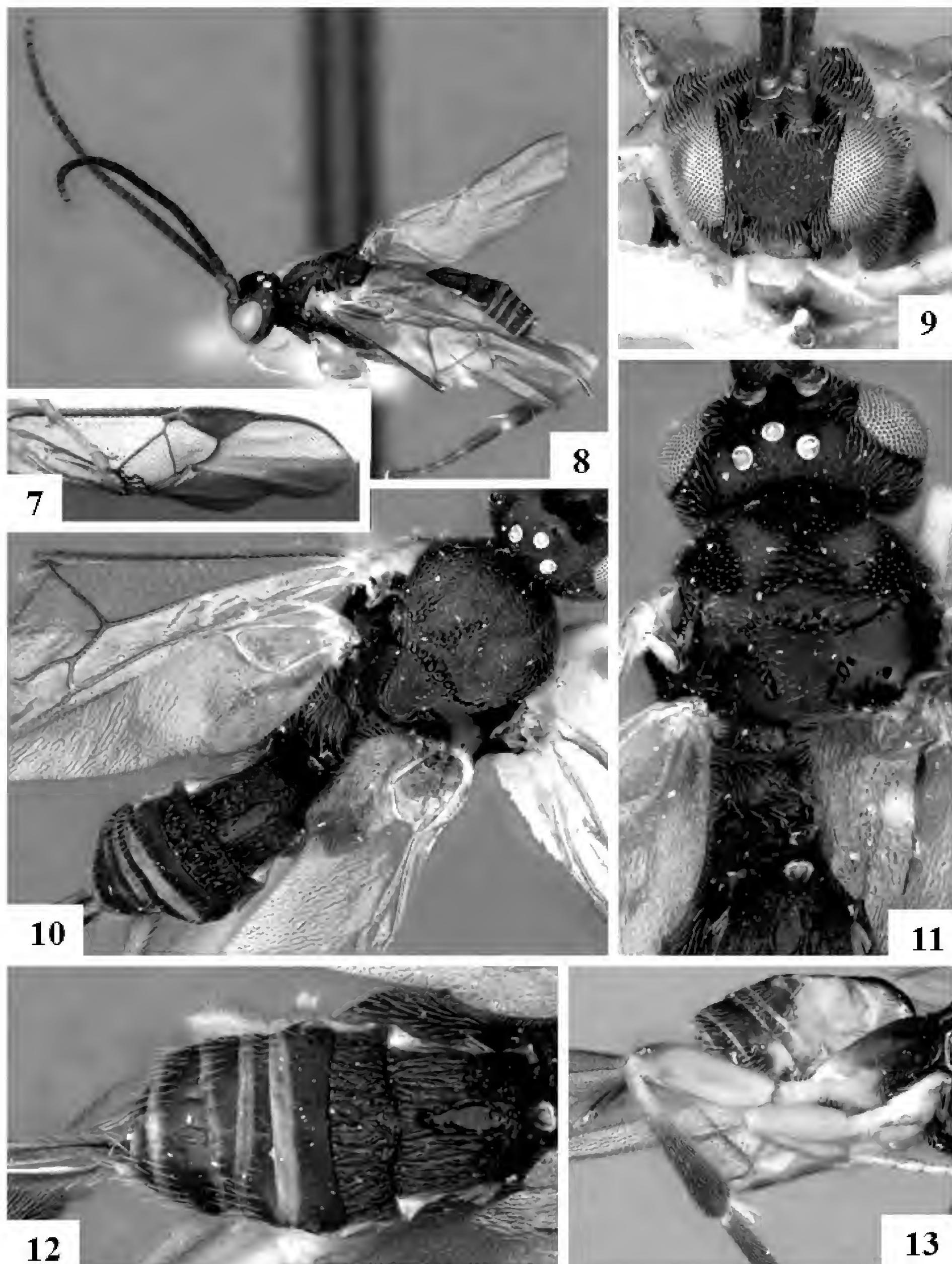
Holotype. Female, NMNH (examined). UNITED STATES: Minnesota, Lake Itasca, Westside across from Biological Station, 28.vii.1963, coll. D. L. Deonier.

Description. Detailed descriptions and images of the species available in Mason (1981) and Valerio et al. (2004).

Biology. Unknown.

Distribution. Canada (Ontario) and United States (Michigan) (Mason 1981, Valerio et al. 2004, Fernandez-Triana 2010).

Comments. Valerio et al. (2004) mentioned that the holotype of this species was in the CNC. However, the NMNH is the institution actually storing the type – see the original description for details (Mason 1981: 41).



Figures 7–13. *Exoryza mariabustosae*, holotype.

***Exoryza monocavus* Valerio & Whitfield, 2004**

Exoryza monocavus Valerio & Whitfield, 2004: 3. Original description.

Holotype. Female, INBio (examined). COSTA RICA: Puntarenas, San Luis, Monte Verde, Buen Amigo, 1,000–1,350m, xi-1994, coll. Z. Fuentes de Luz, LN 250850–449250.

Description. A detailed description and images of the species are available in Valerio et al. (2004).

Biology. Unknown.

Distribution. Known only from the holotype locality in Costa Rica.

***Exoryza reticarina* Song & Chen, 2003**

Exoryza reticarina Song & Chen, 2003: 287. Original description.

Holotype. Female, FAFU (not examined). CHINA: Xishuangbanna, Yunnan, 19-ix-1988, coll. Zhang Liqin.

Description. A detailed description of the species and images are available in Song and Chen (2003).

Biology. Unknown.

Distribution. Known only from the holotype locality in China.

***Exoryza richardashleyi* Fernandez-Triana, sp. n.**

<http://zoobank.org/EA513E18-11FE-4118-B5E7-1EB1A312C20B>
Figs 14–19

Holotype. Female, CNC. COSTA RICA: Guanacaste, ACG, Sector Cacao, Sendero Cima, 1,460m, 10.93328, -85.45729, 18.xii.2008, coll. D. Janzen & W. Hallwachs. DNA voucher code: DHJPAR0031507.

Paratype. 1 #M (CNC). Costa Rica, Alajuela, ACG, same locality than holotype. DNA voucher code: DHJPAR0031469.

Diagnostic description. Head (except for clypeus and mandibles), mesosoma and metasoma (dorsally) dark brown to black; laterotergites, sternites and hypopygium partially yellow, partially dark brown; antennal flagellomeres dark brown; tegula and wing base yellow-brown; pterostigma pale yellow on proximal 0.5, brown on distal 0.5; legs mostly white-yellow except for metacoxa (black on proximal 0.7, white-yellow on distal 0.3), metafemur (distal 0.1 dorsally brown), metatibia (distal 0.2 dark brown, but also with narrow brown band dorsally on distal 0.5), and metatarsus (dark brown). **Body ratios.** Flagellomere 2 length/width: 3.2 x. Flagellomere 14 length/width: 1.5 x. Malar line/mandible width: 0.9 x. Metafemur length/width: 4.1 x. Metatibial inner/outer spur length: 1.1 x. T1 length/width at posterior margin: 1.1 x. T2 length/width at posterior margin: 0.4 x. Ovipositor sheaths length/metatibia length: 1.3 x.

sheath length/metatibia length: 1.3 x (approximate value). **Body measurements (all in mm).** Body length: 3.1. Fore wing length: 3.4. Flagellomere 2 length/width: 0.26/0.08. Flagellomere 14 length/width: 0.105/0.07. Flagellomeres 1/2/3/14/15/16 length: 0.27/0.26/0.25/0.105/0.105/0.14. OOL: 0.14. POL: 0.13. Diameter of posterior ocellus: 0.08. Malar line/mandible width: 0.09/0.10. Metafemur length/width: 0.95/0.23. Metatibia length: 1.10. First segment of metatarsus length: 0.51. Metatibial inner/outer spur length: 0.21/0.19. T1 length/width at anterior margin/width at posterior margin: 0.46/0.34/0.42. T2 length/width at posterior margin: 0.19/0.52. T3 length: 0.19. Ovipositor sheaths length: 1.50 (approximate value).

Male. As female, with slightly smoother sculpture.

Biology. Reared from Gelechiidae (an undetermined species with interim name ‘gelJanzen01 Janzen349’).

Distribution. Costa Rica, Alajuela and Guanacaste provinces, ACG (Sectors Cacao and Rincon Rain Forest), between 980–1,460m.

Etymology. Named in honor of Richard Ashley from Huacas, Nicoya, for his serious enthusiasm for understanding and protecting the wild nature that occurs all around him, and specifically for causing 20 Guanacaste school children and their teachers to begin to share that enthusiasm.

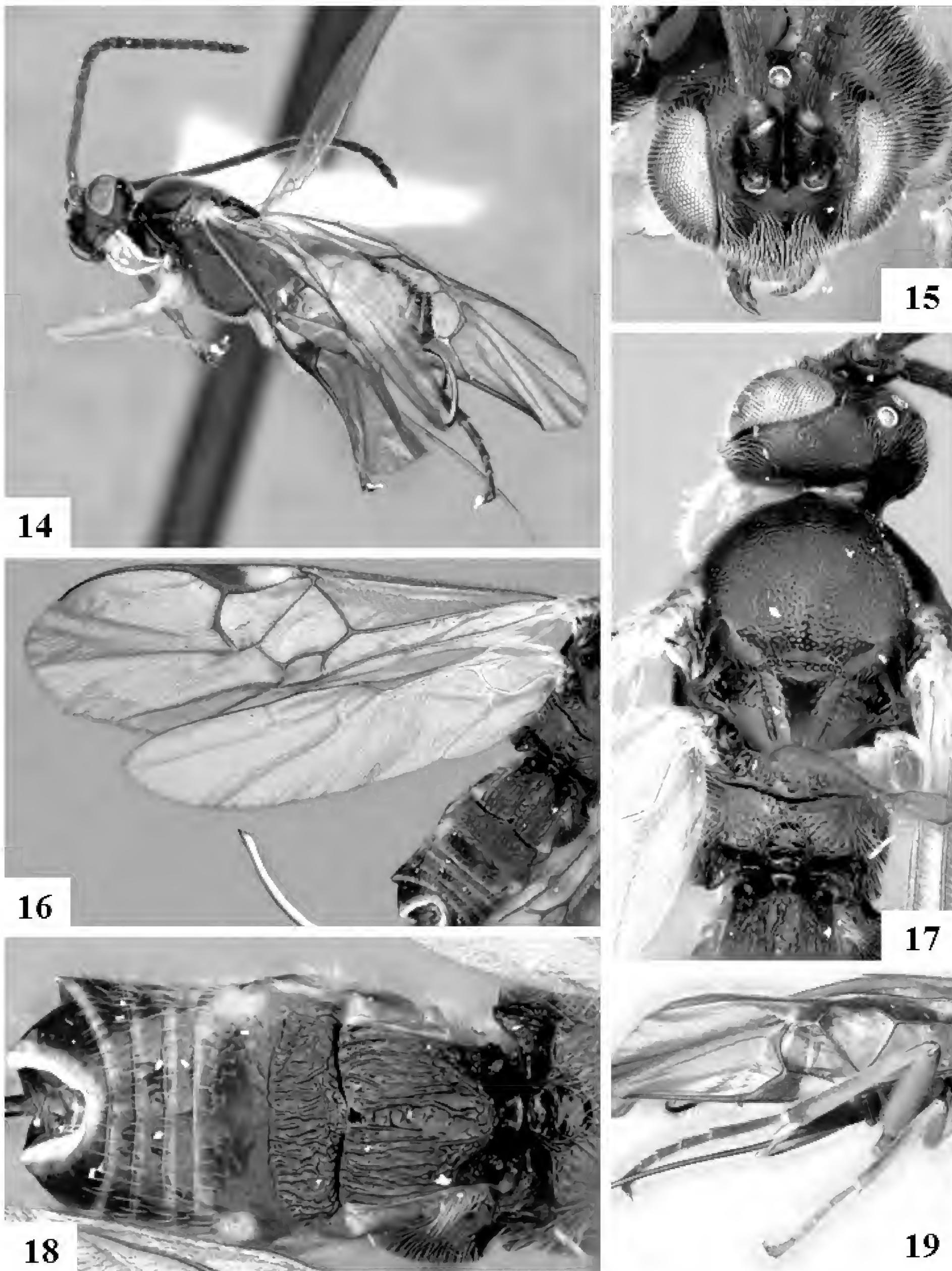
***Exoryza ritaashleyae* Fernandez-Triana, sp. n.**

<http://zoobank.org/1B47AE69-4F7E-439B-A886-346A0DD305E7>
Figs 20–25

Holotype. Female, CNC. COSTA RICA: Guanacaste, ACG, Sector Cacao, Sendero Cima, 1,460m, 10.93328, -85.45729, 18.xii.2008, coll. D. Janzen & W. Hallwachs. DNA voucher code: DHJPAR0031500.

Paratypes. 3 #F (CNC, NMNH). Costa Rica, Guanacaste, ACG, same locality than holotype. DNA voucher codes: DHJPAR0034091, DHJPAR0034103, DHJPAR0034150.

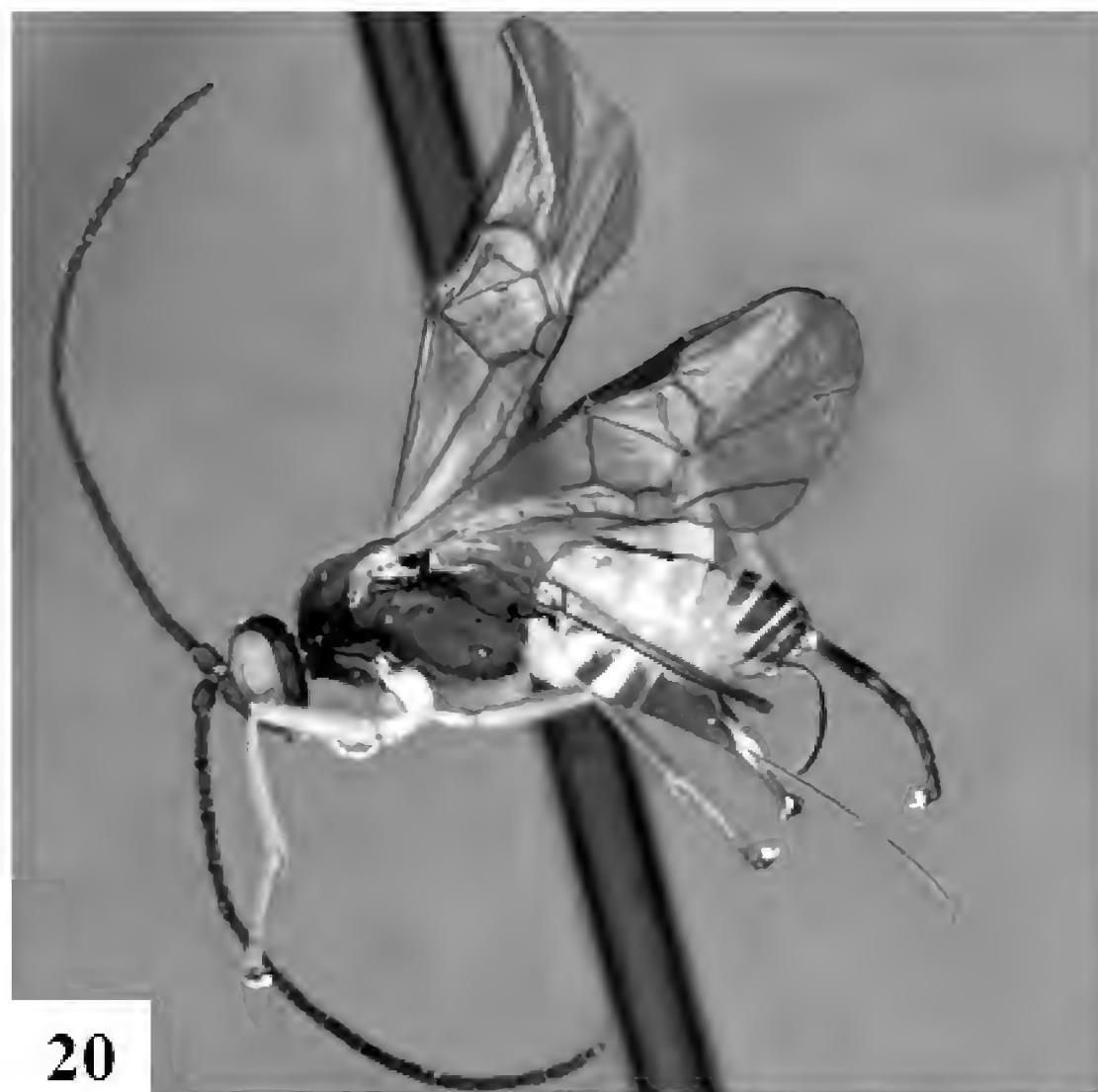
Diagnostic description. Body color. Head (except for clypeus and mandibles), mesosoma and metasoma (dorsally) dark brown to black; laterotergites, sternites and hypopygium partially yellow, partially dark brown; antennal flagellomeres dark brown to black; tegula and wing base yellow-white; pterostigma mostly brown (with small pale spot on proximal 0.1); legs mostly yellow-white except for metacoxa (black on proximal 0.6–0.7, white-yellow on distal 0.4–0.3), metafemur (distal 0.1 dorsally brown), metatibia (distal 0.1 dark brown), and metatarsus (dark brown). **Body ratios.** Flagellomere 2 length/width: 3.5 x. Flagellomere 14 length/width: 1.6 x. Malar line/mandible width: 1.1 x. Metafemur length/width: 3.6 x. Metatibial inner/outer spur length: 1.0 x. T1 length/width at posterior margin: 1.2 x. T2 length/width at posterior margin: 0.4 x. Ovipositor sheaths length/metatibia length: 1.3 x. **Body measurements (all in mm).** Body length: 3.5–3.8. Fore wing length: 3.6–4.1. Flag-



Figures 14–19. *Exoryza richardashleyi*, holotype.

ellomere 2 length/width: 0.30/0.085. Flagellomere 14 length/width: 0.12/0.075. Flagellomeres 1/2/3/14/15/16 length: 0.29/0.30/0.30/0.12/0.11/0.15. OOL: 0.14. POL:

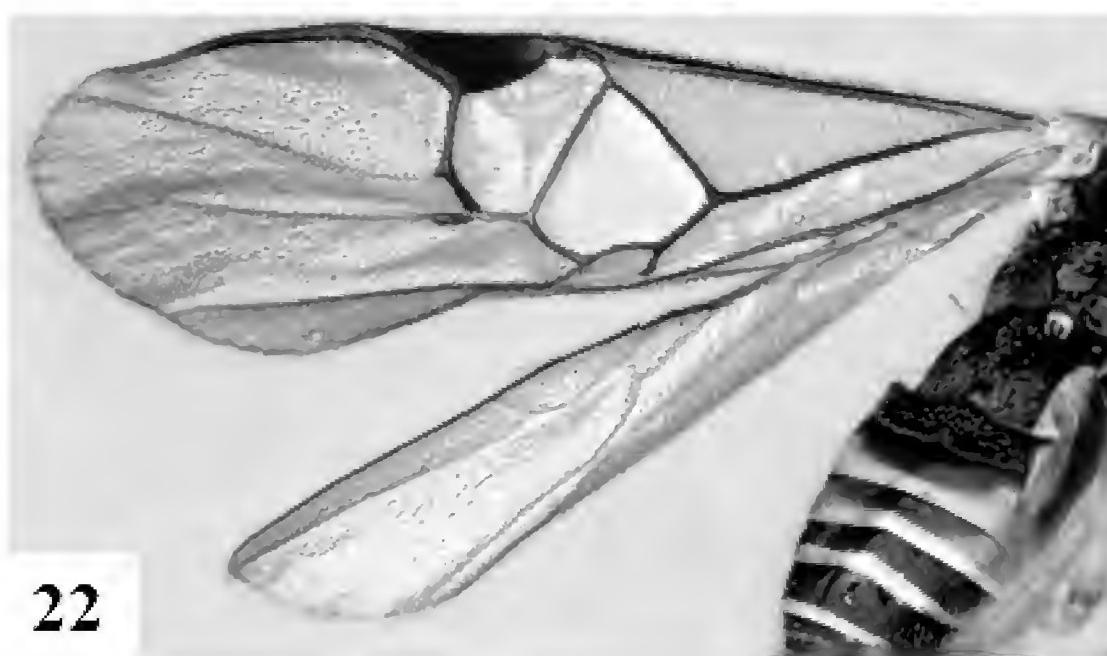
0.12. Diameter of posterior ocellus: 0.08. Malar line/mandible width: 0.11/0.10. Metafemur length/width: 0.98/0.27. Metatibia length: 1.25. First segment of meta-



20



21



22



23



24



25

Figures 20–25. *Exoryza ritaashleyae*, holotype.

tarsus length: 0.57. Metatibial inner/outer spur length: 0.26/0.25. T1 length/width at anterior margin/width at posterior margin: 0.52/0.35/0.42. T2 length/width at

posterior margin: 0.22/0.58. T3 length: 0.21. Ovipositor sheaths length: 1.6–1.9.

Male. Unknown.

Biology. Unknown.

Distribution. Costa Rica, Guanacaste, ACG (Sector Cacao), 1,460m.

Etymology. Named in honor of Rita Ashley from Huacas, Nicoya, for her serious enthusiasm for understanding and protecting the wild nature that occurs all around her, and specifically for causing 20 Guanacaste school children and their teachers to begin to share that enthusiasm.

Exoryza rosamatarritae Fernandez-Triana, sp. n.

<http://zoobank.org/423F126F-DCBB-4F09-81AE-4C3A81C7CEAB>
Figs 26–32

Holotype. Female, CNC. COSTA RICA: Alajuela, ACG, Sector San Cristobal, Finca San Gabriel, 645m, 10.878, -85.393, 18.vi.2013, coll. C. Cano. DNA voucher code: DHJPAR0053053.

Paratypes. 4 #F (CNC, NMNH). Costa Rica, Alajuela, ACG. DNA voucher codes: DHJPAR0033751, DHJPAR0049364, DHJPAR0052979, DHJPAR0053807.

Diagnostic description. Body color. Head (except for clypeus and mandibles), mesosoma and metasoma (dorsally) dark brown to black; laterotergites, sternites and hypopygium partially yellow, partially dark brown; antennal flagellomeres dark brown; tegula and wing base white-yellow; pterostigma mostly brown (with small pale spot on proximal 0.1); legs mostly white-yellow except for metacoxa (black on proximal 0.8, white-yellow on distal 0.2), metafemur (distal 0.2 dorsally brown), metatibia (distal 0.6 dark brown), and metatarsus (dark brown). **Body ratios.** Flagellomere 2 length/width: 3.1 x. Flagellomere 14 length/width: 1.3 x. Malar line/mandible width: 1.0 x. Metafemur length/width: 3.7 x. Metatibial inner/outer spur length: 1.1 x. T1 length/width at posterior margin: 1.1 x. T2 length/width at posterior margin: 0.5 x. Ovipositor sheaths length/metatibia length: 0.8 x. **Body measurements (all in mm).** Body length: 2.5 (2.3–2.8). Fore wing length: 2.7 (2.4–2.8). Flagellomere 2 length/width: 0.22/0.07. Flagellomere 14 length/width: 0.09/0.07. Flagellomeres 1/2/3/14/15/16 length: 0.21/0.21/0.21/0.09/0.09/0.11. OOL: 0.11. POL: 0.10. Diameter of posterior ocellus: 0.06. Malar line/mandible width: 0.09/0.09. Metafemur length/width: 0.66/0.18 (0.65/0.17; 0.74/0.20). Metatibia length: 0.82 (0.82; 0.94). First segment of metatarsus length: 0.41 (0.41; 0.42). Metatibial inner/outer spur length: 0.18/0.16 (0.20/0.18). T1 length/width at anterior margin/width at posterior margin: 0.38/0.28/0.35. T2 length/width at posterior margin: 0.21/0.42. T3 length: 0.18. Ovipositor sheaths length: 0.6–0.8.

Male. Unknown.

Biology. Reared from Choreutidae ('*Brenthia Janzen05*'), Depressariidae ('*Stenoma Phillips543*'), and Gelechiidae (an undetermined species with interim name 'gelJanzen01 Janzen16').

Distribution. Costa Rica, Alajuela, ACG (Sector San Cristobal), 540–645m.

Etymology. Named in honor of Rosa Iris Matarrita Díaz for her enthusiasm in teaching her Colonia Bolaños students to understand and protect the wild nature that occurs in her homeland.

Exoryza schoenobii (Wilkinson, 1932)

Exoryza schoenobii (Wilkinson, 1932): 142. Original description.

Holotype. Female, BMNH (not examined). INDIA: 'South India, Hebbal Farm'.

Description. Detailed descriptions of the species and images are available in Mason (1981) and Valerio et al. (2004).

Biology. Reared from Pyraloidea (*Chilo polychrysa*, *C. suppressalis*, *Glaucocharis reniella*, *Schoenobius bipunctifer*, and *Scirpophaga incertulas*) (Yu et al. 2012).

Distribution. Bangladesh, China (Fujian, Guangdong, Guangxi, Guizhou, Hainan Island, Hubei, Hunan, Jiangsu, Jiangxi, Sichuan, Taiwan, Yunnan, Zhejiang), India, Malaysia, Philippines, Sri Lanka, Vietnam (references summarized in Yu et al. 2012).

Comments. Although the holotype was not examined, we studied two CNC specimens that were compared with the holotype by Mason (Mason 1981, Valerio et al. 2004).

Exoryza safranum Rousse & Gupta, 2013

Exoryza safranum Rousse & Gupta, 2013: 530. Original description.

Holotype. Female, MNHN (not examined). REUNION: Plaine des Palmistes/Grand Etang, xi-2010, coll. T. Ramage.

Description. A detailed description of the species and images are available in Rousse and Gupta (2013).

Biology. Unknown.

Distribution. Known only from the holotype locality in Réunion.

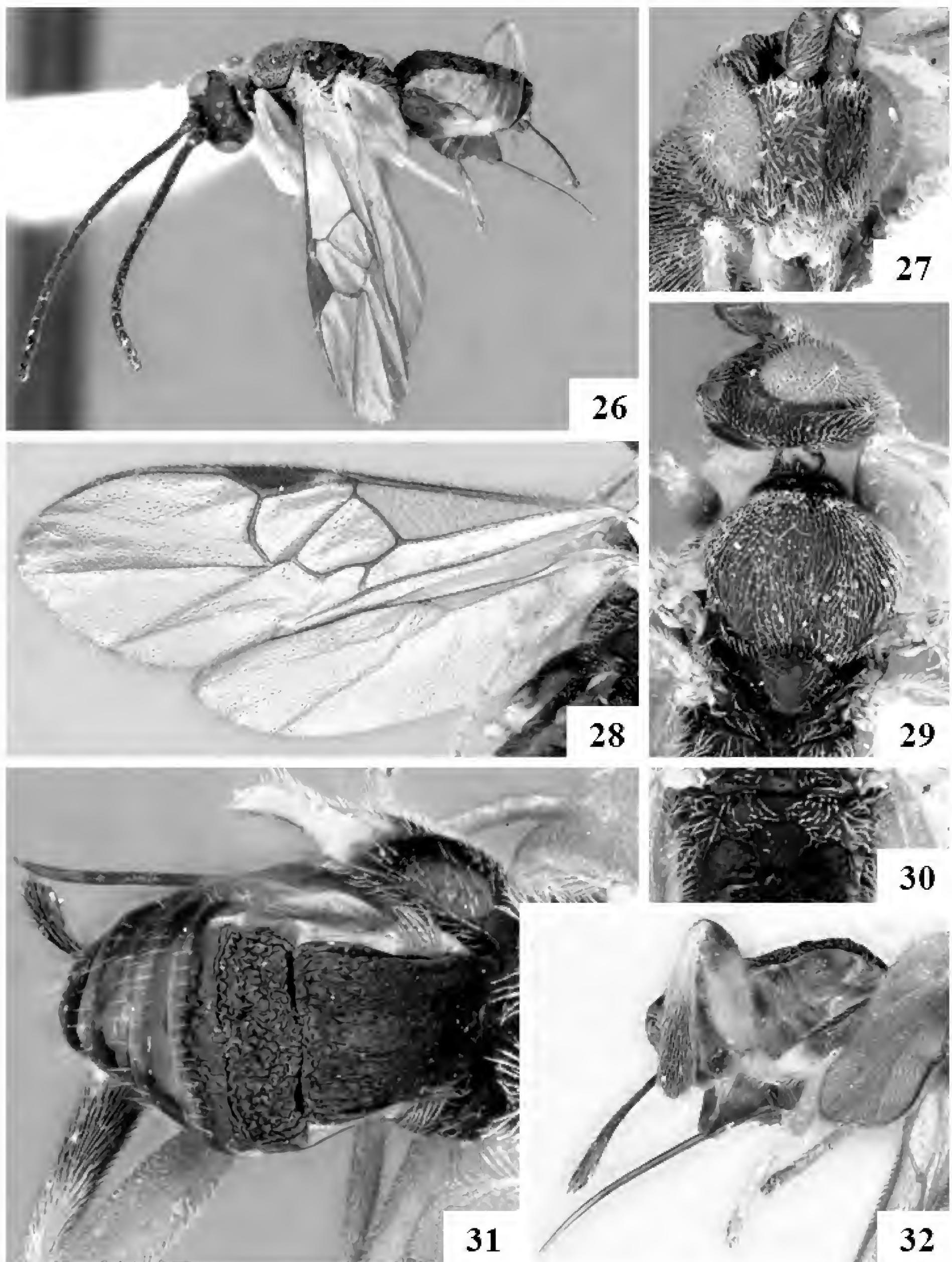
Comments. This species was collected with a light trap.

Exoryza yeimycedenoae Fernandez-Triana, sp. n.

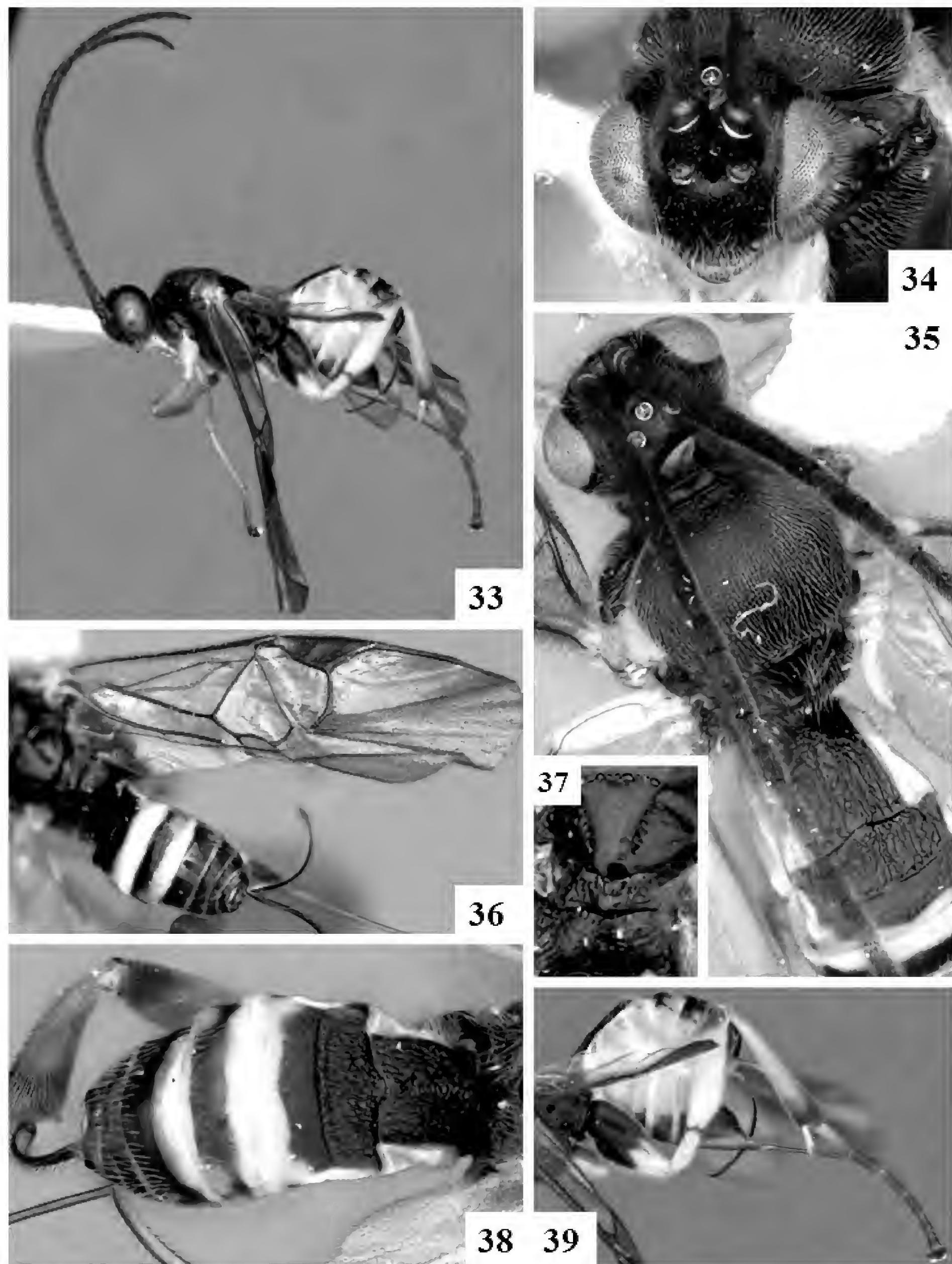
<http://zoobank.org/D659373B-3BF5-4E7F-A580-17488460A972>
Figs 33–39

Holotype. Female, CNC. COSTA RICA: Guanacaste, ACG, Sector Cacao, Sendero Cima, 1,460m, 10.93328, -85.45729, 18.xii.2008, coll. D. Janzen & W. Hallwachs. DNA voucher code: DHJPAR0031496.

Diagnostic description. Body color. Head (except for clypeus and mandibles), mesosoma and metasoma (dorsally) dark brown to black; laterotergites and sternites mostly yellow, hypopygium mostly dark brown; antennal flagellomeres dark brown; tegula and wing base white-yellow; pterostigma mostly brown (with small pale



Figures 26–32. *Exoryza rosamatarritae*, holotype.



Figures 33–39. *Exoryza yeimycedenoae*, holotype.

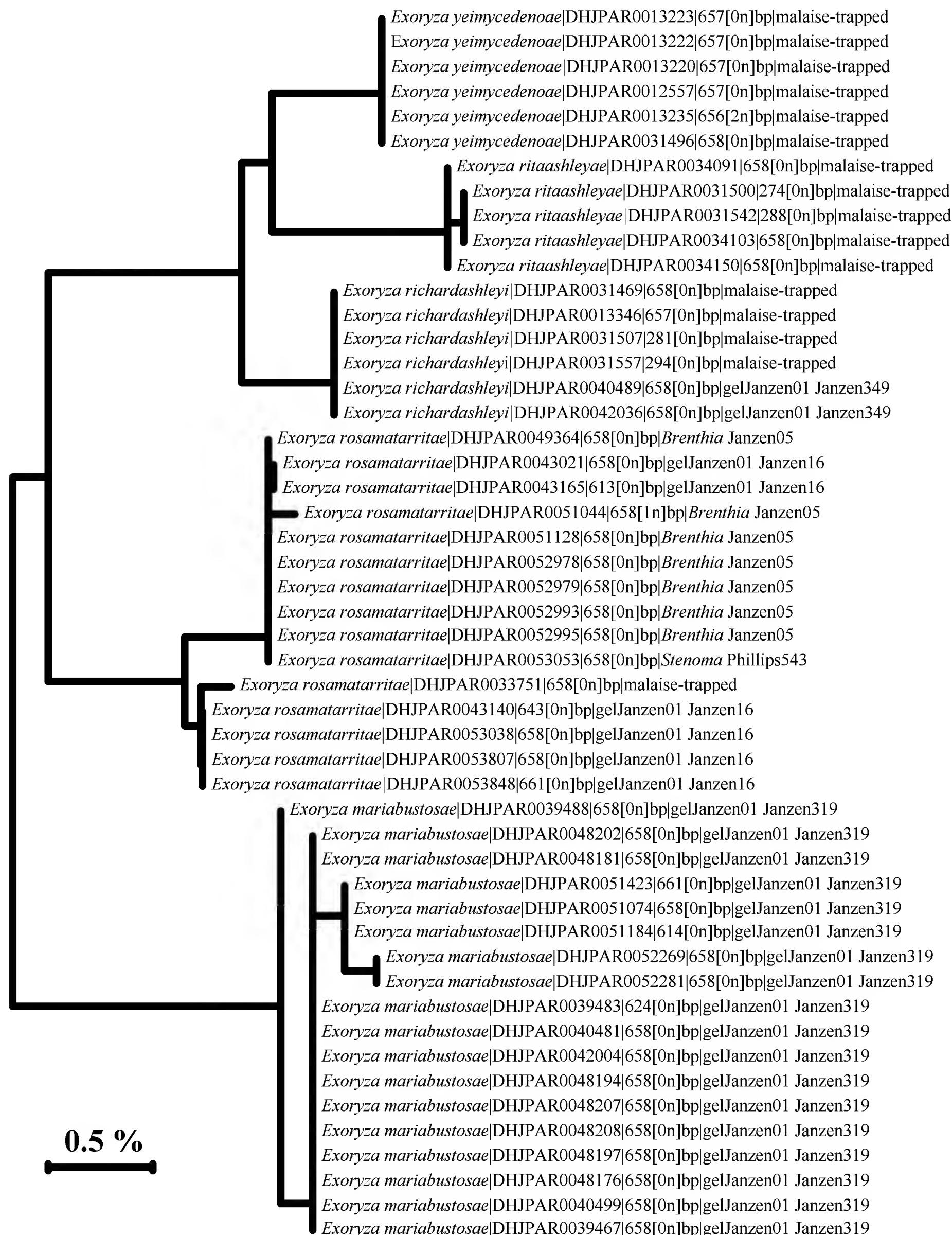


Figure 40. Neighbor-Joining (NJ – Saitou and Nei 1987) tree based on Kimura 2-parameter distances (K2P – Kimura 1980) made using BOLD (Ratnasingham and Hebert 2007) for all barcoded specimens from each of the five species of *Exoryza* in ACG. Tip labels include species name, specimen accession number, sequence length and host species.

spot on proximal 0.1); legs mostly white-yellow except for metacoxa (black on proximal 0.6, white-yellow on distal 0.4), metafemur (distal 0.1 dorsally brown), metatibia (distal 0.2 dark brown), and metatarsus (mostly dark brown). **Body ratios.** Flagellomere 2 length/width: 3.3 x. Flagellomere 14 length/width: 2.1 x. Malar line/mandible width: 0.9 x. Metafemur length/width: 3.8 x. Metatibial inner/outer spur length: 1.1 x. T1 length/width at posterior margin: 1.4 x. T2 length/width at posterior margin: 0.5 x. Ovipositor sheaths length/metatibia length: 1.1 x. **Body measurements (all in mm).** Body length: 3.3. Fore wing length: 3.5. Flagellomere 2 length/width: 0.30/0.09. Flagellomere 14 length/width: 0.14/0.065. Flagellomeres 1/2/3/14/15/16 length: 0.29/0.30/0.30/0.14/0.13/0.165. OOL: 0.13. POL: 0.12. Diameter of posterior ocellus: 0.07. Malar line/mandible width: 0.09/0.10. Metafemur length/width: 0.98/0.26. Metatibia length: 1.17. First segment of metatarsus length: 0.60. Metatibial inner/outer spur length: 0.28/0.25. T1 length/width at anterior margin/width at posterior margin: 0.50/0.33/0.35. T2 length/width at posterior margin: 0.24/0.48. T3 length: 0.19. Ovipositor sheaths length: 1.3.

Biology. Unknown.

Distribution. Costa Rica, Guanacaste, ACG (Sector Cacao), 1,460m.

Etymology. Named in honor of Yeimy Cedeño Solís for her enthusiasm in encouraging her Area de Conservación Tempisque community to understand and protect the wild nature that occurs in her homeland.

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Cyphocoleus Chaudoir (Coleoptera, Carabidae, Odacanthini): descriptive taxonomy, phylogenetic relationships, and the Cenozoic history of New Caledonia

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<http://zoobank.org/45552C4E-C6AE-4F94-9998-0C2D492333B3>

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Abstract

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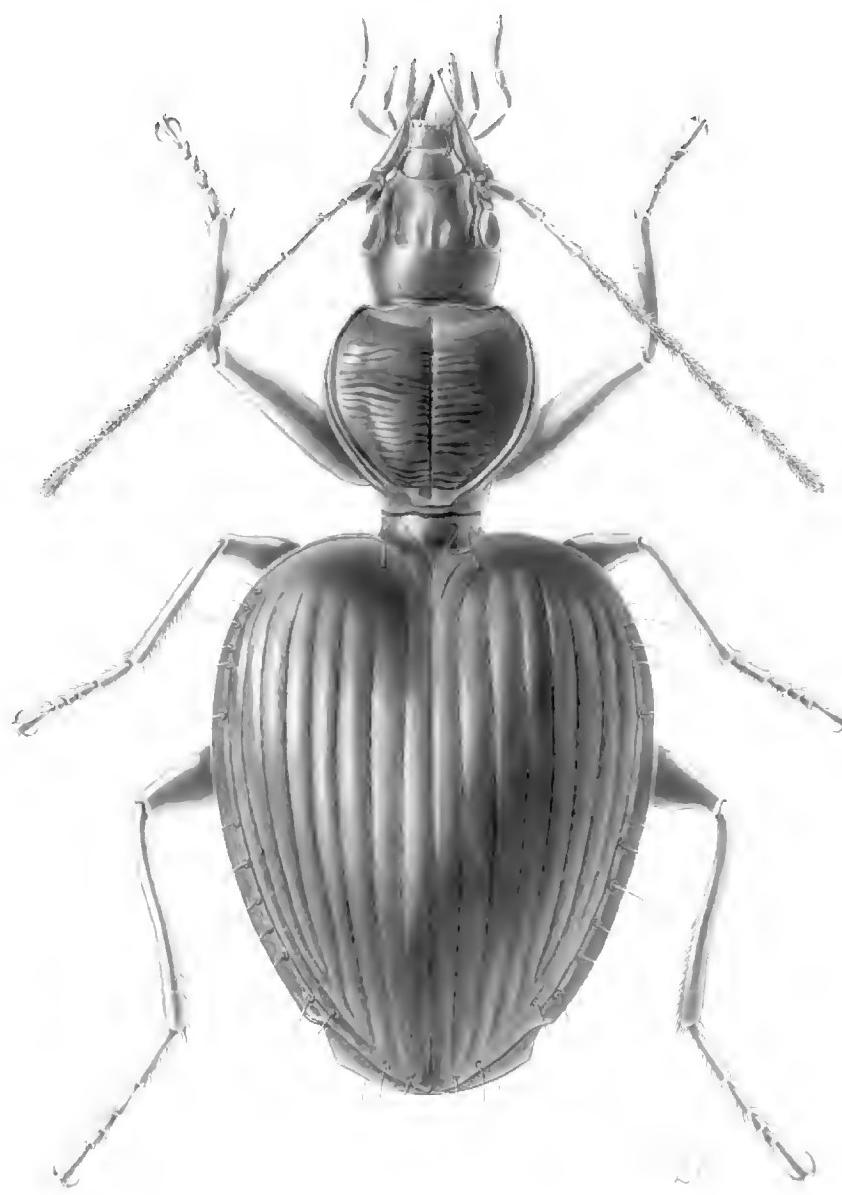
Antarctica
biogeography
morphology
revisionary systematics
taxonomic revision

The precinctive New Caledonian genus *Cyphocoleus* Chaudoir is revised with 22 species recognized, 12 newly described: *C. lissus* sp. n., *C. prolixus* sp. n., *C. parovicollis* sp. n., *C. burwelli* sp. n., *C. angustatus* sp. n., *C. monteithi* sp. n., *C. fasciatus* sp. n., *C. lescheni* Liebherr & Will, sp. n., *C. cordatus* sp. n., *C. bourailensis* sp. n., *C. subulatus* sp. n., and *C. iledespinsensis* sp. n. *Atongolium* Park & Will is found to be a junior synonym of *Cyphocoleus*, with its two species recombined as *C. mirabilis* comb. n. and *C. moorei* comb. n. Results of a survey of Harpalinae Bonelli place *Cyphocoleus* as a member of Odacanthini based on synapomorphies of the eighth abdominal tergite and the female spermathecal assembly. *Cyphocoleus* shares with five other generic-level taxa – *Homethes* Newman, *Aeolodermus* Andrewes, *Stenocheila* Laporte, *Quammenis* Erwin and *Diplacanthogaster* Liebke – a single-segmented maxillary galea that is appressed to the outer margin of the maxillary lacinia. These six generic-level taxa are newly classified as members of subtribe Homethina subtrib. n. (type genus *Homethes*). Cladistic analysis including 79 taxa and utilizing 119 morphological characters supports division of Odacanthini into four monophyletic subtribes: 1, Actenonyicina (*Actenonyx* White); 2, Homethina; 3, Pentagonalina (*Pentagonica* Dana, *Parascopodes* Darlington, *Scopodes* Erichson); and 4, Odacanthina (24 genera in this analysis monophyletically defined by *Lasiocera* Dejean and its adelphotaxon). These subtribes are phylogenetically arranged as: (Actenonyicina (Homethina (Pentagonalina + Odacanthina)). Area relationships defined within Homethina – (New Caledonia (Australia (South America + Central America))) – support the origin of New Caledonian *Cyphocoleus* prior to amphantarctic vicariance between South America and Australia. Consistent with previous molecular dating of 100–105 Ma for the origin of Odacanthini, a general vicariance-based hypothesis proposes that New Zealandian *Actenonyx* and New Caledonian *Cyphocoleus* were emplaced on Zealandia prior to the completion of rifting between Zealandia and Australia during Late Cretaceous, and that both fragments of Zealandia remained subaerial throughout the Cenozoic. Alternatively, under a very specific time-constrained biogeographic hypothesis laden with an added assumption of dispersal, the ancestor of *Cyphocoleus* could have colonized New Caledonia during a 2–5 Ma period after its proposed subaerial reemergence at 37 Ma. A clade within *Cyphocoleus* synapomorphously exhibits an environmental patina: a varnish-like coating to the dorsal body surface that is hypothesized to enable crypsis of the adult beetle. Several specializations of elytral setae are also synapomorphies of this clade, suggesting evolutionary association of the patina and the setal specializations.

Introduction

When Baron Maximilien de Chaudoir (1877) described the genus *Cyphocoleus*, he wrote “Ce genre présente plusieurs particularités ... Sa place est assez difficile à préciser (p. 196).” He went on to suggest several tentative affinities: “il se rapproche des *Oxyglossus*; il ne rentre bien ni dans les Anchoménides, ni dans les Thyréoptérides, et constitue une forme intermédiaire entre des deux groupes (genus osculans) (p. 196).” Thus he was conflicted as to whether the genus should be classified as Anchoménides (tribe Platynini), or as Thyréoptérides (subtribe Pericalina of Lebiini of which *Oxyglossus* is a member) (Shpeley and Ball 2001). Given that Chaudoir described *Cyphocoleus* when he was 61 years old – after he had visited major insect collections at Oxford, London, Leiden, Brussels, Paris, Berlin, Genova, and Prague, had acquired specimens from collections developed by numerous authors, e.g. Bates, Dejean, La Ferté de Sénectère, Waterhouse, Wollaston, and had corresponded and discussed carabid beetles with many leading lights of his day (Basilewsky 1983, Ball and Erwin 1983) – his indecision regarding the placement of the new genus is remarkable. This indecision was partly based on lack of material, as he described his new genus and three new species from three specimens. He also acknowledged that New Caledonia, whence *Cyphocoleus* are precinctive, “fourni déjà tant de formes curieuses et spéciales [furnished already so many curious and special forms] (Chaudoir 1877, p. 196).” That *Cyphocoleus* beetles, with their bizarre physiognomy (Fig. 1) represent some of those “curious and special forms” may explain a connection that Chaudoir failed to make. In describing *Cyphocoleus* he noted the unsegmented galea, or outer lobe, of the maxilla. This observation is in keeping with his attention to the details of carabid beetle maxillae in this studies (Ball and Erwin 1983). He had previously also noted this condition in the Austral-Pacific genus *Homethes* Newman and the South American genus *Stenocheila* Laporte (Chaudoir 1872). But in 1877 he made no connection between *Cyphocoleus*, *Stenocheila*, and *Homethes*. Below it is shown that these taxa plus the genera *Aeolodermus* Andrewes (1929) [treated as *Homethes* in Chaudoir, 1872], *Diplacanthogaster* Liebke (1932) and *Quammenis* Erwin (2000), all of whom synapomorphously share an unsegmented maxillary galea, comprise a newly recognized monophyletic taxon.

Chaudoir’s first stated yet tentative placement of *Cyphocoleus* in tribe Platynini was summarily adopted by the only other species describer and reviser of the group (Fauvel 1882). These beetles remained rarely collected throughout the 19th and much of the 20th century. Prior to E. O. Wilson’s expedition to New Caledonia in 1955 (Fig. 1), 20th Century *Cyphocoleus* collections included 11 specimens (6 species, 2 newly described below) from the Sarasin and Roux (1911) Zoological Expedition (for other taxa see Sarasin and Roux 1913–1918), 7 specimens (2 species, 1 newly described) collected by P. D. Montague in 1914 (Turner 1919), and 9 specimens (3 species, 1 new-



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Figure 1. *Cyphocoleus subulatus* sp. n. male paratype dorsal view: NEW CALEDONIA, Ciu, near Mt. Canala, 300 m el., 1–3–i–1955, rainforest, E. O. Wilson (MCZ).

ly described) collected in 1944 by J. C. Herron during the Allied Forces’ occupation (Alexander 1948). Comprehensive taxonomic revision of *Cyphocoleus* is now possible based on field specimens collected by Dr. G. B. Monteith and his Queensland Museum colleagues over the past 30 years, with those samples taken from a wide range of localities visited over nearly 90 collecting days.

This revision aims primarily to delineate and describe the species that comprise *Cyphocoleus*. Taxonomic placement of the genus is based on cladistic analysis using morphological characters of the adult beetles. Comprehensive character analysis of *Cyphocoleus* shows clearly that these species are members of the tribe Odacanthini. Moreover, within Odacanthini, *Cyphocoleus* and five other genera form a monophyletic group defined in part by a remarkably salient character: a one-segmented maxillary galea that lies appressed to the outer margin of the maxillary lacinia. Its evolution may be an evolutionary specialization associated with elongation of the mandibles in these beetles, as a similar maxillary configuration – a one-segmented galea that is held free apically from the lacinia – is observed in the long-jawed bembidiine genus *Amerizus* Chaudoir (1868). However, a single segmented galea is also present in members of tribe Callistini (Chaudoir 1872), though these beetles exhibit only moderately elongated mouthparts: i.e. mandibles and maxillae. And a single-segmented galea is pres-

ent in *Monolobus* Solier of the tribe Migadopini, beetles of that genus exhibiting short mandibles (Jeannel 1938). Numerous other characters also support this newly recognized clade – classified as subtribe Homethina subtrib. n. – and place the lineage as an early offshoot within Odacanthini. Biogeographic relationships within Homethina are amphianarctic, with other member genera occupying Australia, tropical South America, and Central America. It is proposed that these amphianarctic biogeographic relationships are of Cretaceous age, and therefore associated with the fragmentation of Gondwana. This hypothesis necessitates that *Cyphocoleus* spp. have occupied a subaerial New Caledonia throughout the Cenozoic: i.e. over the past 60 Ma. The consequences of such a hypothesis are discussed in light of molecular dating studies of carabid beetles (Ober and Heider 2010) and the phylogenetic and biogeographic relationships among the various subtribal lineages that comprise Odacanthini.

Materials and methods

Taxonomic material. The taxonomic revision of *Cyphocoleus* is based on 826 specimens borrowed from 19 institutions (see Acknowledgements). All type specimens were examined for 20 of the 22 species. For two species – *Cyphocoleus mirabilis* (Park & Will) and *C. moorei* (Park & Will) – a paratype specimen (QMB) was compared to recently collected material to verify the identifications. Specimens representing outgroups of *Cyphocoleus* represented in the cladistic analysis were obtained from other institutions listed in the Acknowledgements (see Suppl. material 1). Holotypes for all newly described species are deposited in MNHN, Paris. Lectotypes are designated for those species described from a syntype series. Information on primary type labels is reported verbatim from the specimen labels, with separate lines of text on a label demarcated by a single slash (/), and separate labels by a double slash (//). All label text is presented as non-italics, as per the printed or handwritten labels themselves.

Laboratory techniques. Standard light microscopy, dissection and staining protocols used in this study are described in Liebherr (2015: 18–20). The major exception involves dissection of male genitalia, where both abdominal segments VIII and IX were removed, along with the male aedeagus, from the male abdomen during this study. This procedure allowed examination of mediotergite VIII and the position of the associated spiracles in beetles of the studied taxa. These segments are routinely removed together in female dissections, along with the female reproductive tract, and in some instances the female tergites and ventrites of abdominal segment VIII were slide mounted in glycerine for microscopic examination. The vast majority of beetles studied were prepared in dry-mounted condition on pins or points. A small minority of specimens are maintained in 100% ethanol; these specimens were determined and labeled just as the dry material.

Descriptive conventions. All ingroup *Cyphocoleus* specimens were determined to species through comprehensive examination, including both external characteristics and male genitalia. In order to assess the latter in a comprehensive manner, males of most collecting series, and in some instances numerous males, were dissected. The dissected males were labeled in succession as “male 1, male 2, ...”, with these working labels retained on the specimens along with the genitalia stored in polyethylene genitalia vials. Once specimens had been sorted to species, five specimens (or as many as possible for more rarely collected species) were chosen for mensural analysis. The five specimens included the largest and smallest beetle for the species, plus a representation of males and females. These specimens were labeled as “measured specimen 1 ...” and subjected to intensive examination of external characters. Based on the sample specimens, body size range, and variation among various body ratios were estimated. Also, qualitative characters were assessed among the five to ensure consistency among the specimens sorted to species. All data were entered into multiple Excel® spreadsheet pages, with these data serving as the basis for the dichotomous key, diagnoses, and descriptions.

Several measurements proved useful for diagnosing species. Eye development was quantified by the ocular ratio: MHW/mFW, or maximum head width across eyes divided by the minimum frons width between eyes. Dimensions of the pronotum were routinely used to diagnose several of the species, with four measurements made: 1, MPW, maximum pronotal (or prothoracic) width, measured either across the pronotum, or across the externally bulging proepisterna if visible in dorsal view; 2, APW, apical pronotal width, measured between the two most anterior points along the front of the pronotum; 3, BPW, basal pronotal width, measured across the base of the pronotum along the lateral marginal bead; and 4, PL, pronotal length, or the distance from the apex of the pronotum to the basal margin measured along the midline. These measurements were variously combined into the ratios APW/BPW, MPW/BPW, and MPW/PL, in order to describe prothoracic configuration. The ranges of these ratios are used for descriptive purposes only without any statistical connotations.

Three measurements of the elytra were also used to describe body shape: 1, MEW, maximal elytral width; 2, HuW, humeral width, or the distance between the anterior-most points along the basal elytral margin on both sides of the scutellum; and 3, EL, elytral length, or the distance from the base of the scutellum to the elytral apex, measured parallel to the fused suture, and to the farther of the two apices if they are separated by a median invagination at the suture. These measurements were combined into two ratios, MEW/EL, and MEW/HuW. The former describes the relative elytral breadth, whereas the latter ratio describes the relative width at the front of the elytra, i.e. the humeral development, versus the maximal elytral width near the elytral midlength.

Variation among individuals for counts and relative positions of the lateral elytral setae – i.e. those setae present in the broadened eight elytral interval – is presented using the convention of a(b) + c + d(e). In this sequence, “a” represents the modal number of setae in the anterior series of lateral elytral setae commencing just laterad the humerus, and “(b)” represents the number of setae in the minority of specimens, assuming there is variation observed. The value “c” is used if a seta is isolated between the anterior and posterior series of lateral setae. And “d” represents the modal number of setae in the posterior series of lateral elytral setae situated just anterad the elytral subapical sinuation, with “(e)” representing the number of setae in the minority of specimens for this setal series, assuming variation is observed.

Standardized body length used to describe body size is the sum of three measurements: 1, head length measured from the labral medioapical margin to the cervical ridge at the head-pronotal juncture; 2, pronotal length as measured above; 3, elytral length as measured above. As this sum of measurements ignores the apical portion of the elongate mandibles (always in variable positions specimen to specimen) and any distended portions of the abdomen (also variable dependent on specimen condition when prepared), the standardized body length measure will be smaller than the size perceived by eye.

Results

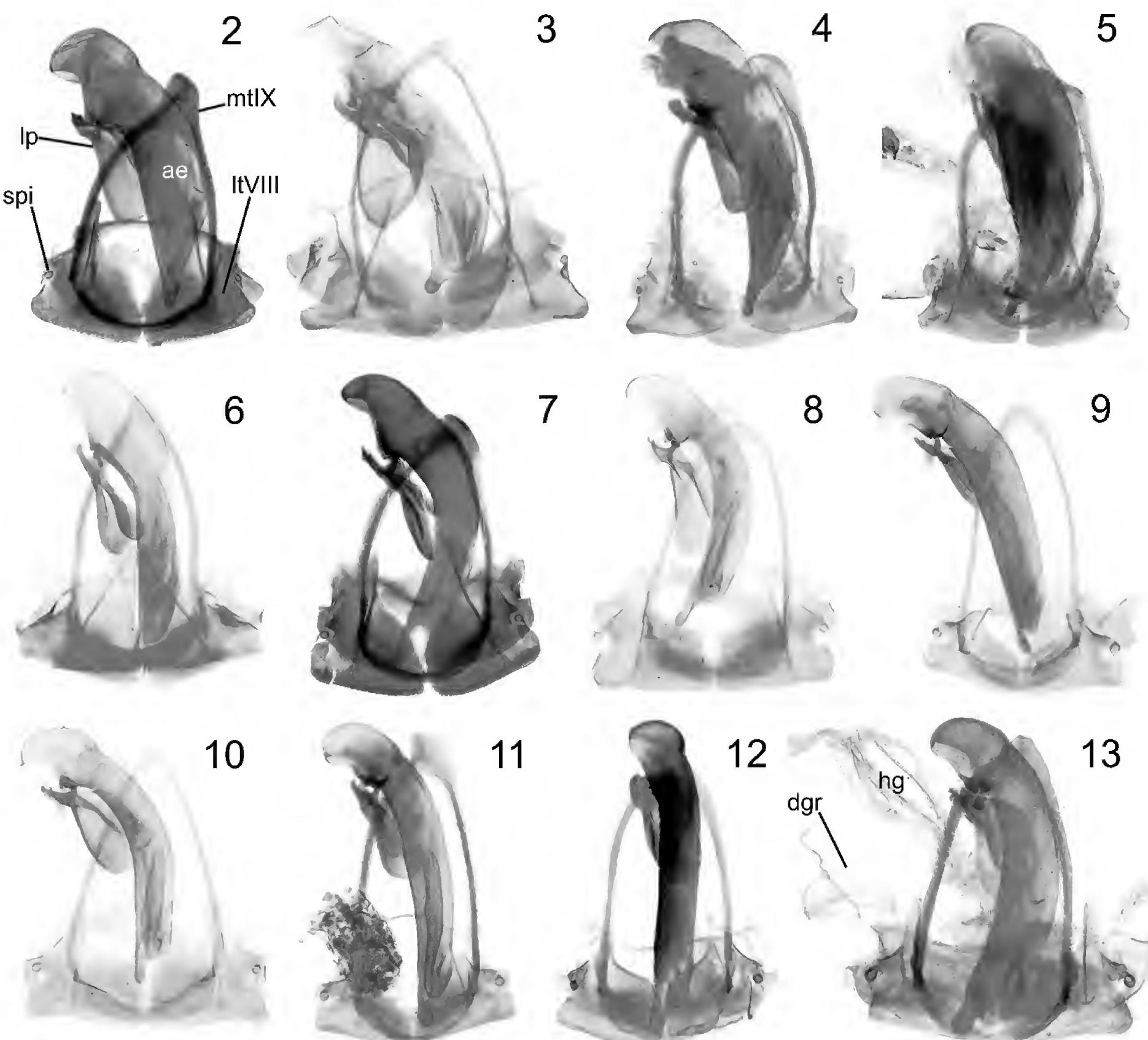
Ingroup circumscription. The principal intents of this study are to revise the species-level taxa assigned to *Cyphocoleus*, and to deduce the phylogenetic relationships of those taxa. The latter goal requires robust definition of outgroup taxa to be included in the phylogenetic analysis of *Cyphocoleus*. This task was complicated by the variety of published proposals regarding taxa found in this study to be related to *Cyphocoleus*. The female reproductive tract of *Cyphocoleus* supports inclusion of the genus in Odacanthini, as the spermathecal assembly exhibits a unique configuration (Figs 35–43, 60–65), wherein the spermatheca is composed of two parts, an apical and basal bulb, that attach to a spermathecal basal sclerite. This sclerite arcuately joins the common oviduct (Fig. 39). Liebherr (1990) found that this configuration characterizes the genera *Homethes* Newman and *Aeolodermus* Andrewes, necessitating transfer of those genera from Tribe Platynini Bonelli to Odacanthini Laporte. Based on a simplified cladistic analysis, Liebherr (1990) also transferred the genera *Pentagonica* Dana and *Scopodes* Erichson to Odacanthini, thereby synonymizing Tribe Pentagonalicini Bates. This proposal was not unanimously accepted, with the pentagonalines either maintained as a subtribal entity (Lorenz 2005), or as a distinct tribe (Bousquet 2012). Previously Liebherr (1988) proposed the superfamily Odacanthitae to include the tribes Odacanthini and Lachnophorini, the member taxa of these taxa characterized by a bipartite spermatheca. Liebherr

and Will (1998) provided an expanded taxonomic survey of female reproductive tract characters, proposing 11 genera – including *Pentagonica*, *Scopodes*, and *Cyphocoleus* – as members of Odacanthini. They also proposed that the bipartite spermathecal configuration observed in Odacanthini was homologous to that observed in Lachnophorini, indicating a sister-group relationship between these tribes. This phylogenetic scheme was followed by Erwin and Zamorano (2014), who proposed three lineages to comprise the supertribe Odacanthitae: Odacanthini, Lachnophorini LeConte, and Calophaenini Jeannel. Within their classification, five genera were placed *incertae sedis* within Lachnophorina: *Homethes*, *Aeolodermus*, *Stenocheila*, *Diplacanthogaster* Liebke, and *Selina* Motschulsky.

Based on DNA molecular sequence data, Ober and Maddison (2008) presented a starkly different hypothesis for the phylogenetic relationships of these taxa. In their maximum likelihood 28Sbe + wg dataset (Ober and Maddison 2008, fig. 2), Odacanthini comprise the sister group to Peleciini, whereas the distantly related Lachnophorini are the adelphotaxon to the various panagaeite lineages (Chlaeniini Brullé, Oodini La Ferté-Sénectère, Panagaeini Bonelli, and Licinini Bonelli). Dating the molecular divergences of these various lineages puts the incongruity in temporal terms, with divergence of the two tribes, plus the tribe Platynini Bonelli, at well over 100 Ma (Oder and Heider 2010). The molecular data agree with the previous synonymy of Pentagonalicini and Odacanthini as the pentagonaline exemplar taxa (*Pentagonica*, *Scopodes*, and *Actenonyx* White) and odacanthine representatives were found to be reciprocally paraphyletic (Ober and Maddison 2008: fig. 2).

These starkly different sets of results suggest the need for reevaluation of the previously proposed relationship of Lachnophorini and Odacanthini based principally on spermathecal configuration. Whether to include lachnophorine taxa as outgroups for the phylogenetic analysis of *Cyphocoleus* formed the proximate question in this endeavor. More broadly, an anatomical survey of taxa placed in Lachnophorini and Odacanthini was undertaken to allow a robust circumscription of taxa to be assigned to Odacanthini. By necessity, such circumscription must precede cladistic analysis of the constituent taxa.

In a seminal morphological analysis of the abdominal terminalia of Carabidae, Deuve (1993) studied the mediotergite VIII of a variety of taxa across Harpalinae. He found that the eighth mediotergite was plesiomorphically continuous medially, with several taxa exhibiting a derived membranous median division of the sclerite. Lachnophorini share the continuous, plesiomorphic mediotergite with taxa in Platynini, Chlaeniini, Abacetini Chaudoir, Hexagoniini G. Horn, and various zuphiite tribes (Dryptini Bonelli, Zuphiini Bonelli, and Galeritini Kirby) (Deuve 1993: 95). Conversely, *Pentagonica* shares with various lebiite genera (*Peliocypas* Schmidt-Göbel, *Pseudomasoreus* Desbrocher des Loges, and *Eurydera* Laporte) the derived, mediotergite condition wherein it is divided into two laterotergites.

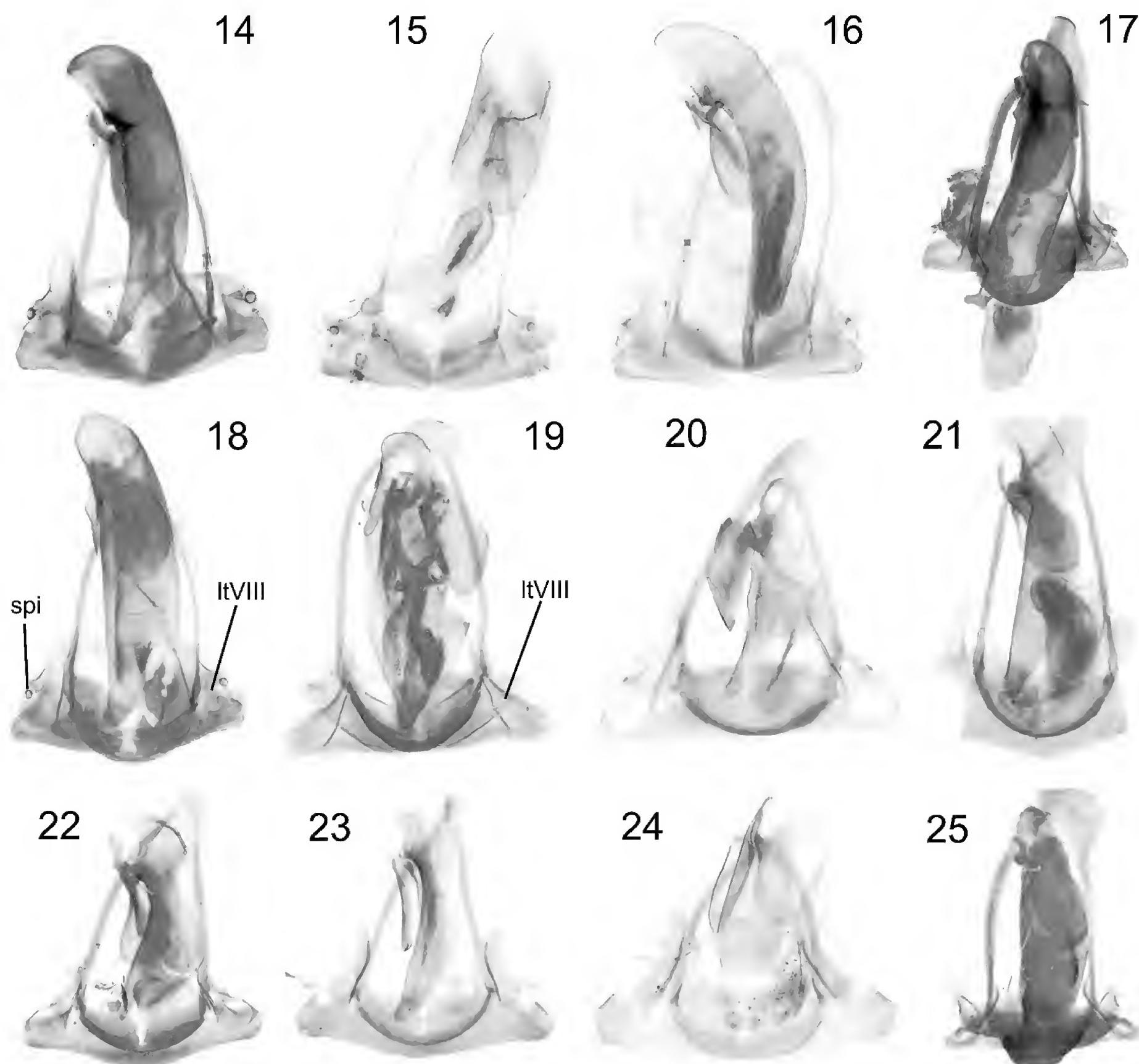


Figures 2–13. Male aedeagus with associated abdominal segments VIII and IX, dorsal view, for taxa assigned to Odacanthini (see Suppl. material 1): **2**, *Actenonyx bembidioides*; **3**, *Homethes guttifer*; **4**, *Quammenis spectabilis*; **5**, *Stenocheila lacordairei*; **6**, *Pentagonica daimella*; **7**, *Scopodes edwardsii*; **8**, *Lasiocera orientalis*; **9**, *Eucolliuris fuscipennis*; **10**, *Renneria kamouni*; **11**, *Arame macra*; **12**, *Odacantha melanura*; **13**, *Deipyrodes palustris*. For abbreviations see Table 1.

Given this distinctive difference in abdominal configuration, abdominal segments VIII and IX and associated male genitalia were dissected from a variety of taxa previously assigned to Odacanthini and Lachnophorini (Figs 2–25). Based on the molecular results placing *Actenonyx* with pentagonaline taxa, as well as earlier suggestions of affinities between *Actenonyx* and Odacanthini (Britton 1941, Liebherr 1988), *A. bembidioides* White was included and found to exhibit the derived, mediotergite divided into paired laterotergites VIII (Fig. 2). Moreover, the spiracle of abdominal VIII was found to be incorporated into the lateral portion of the laterotergite, where it is surrounded by a narrow membranous lunule (Fig. 2). The genera *Pentagonica* and *Scopodes* (Figs 6, 7) also exhibit this condition, as do other taxa consistently included within Odacanthini (Figs 8–18). Three other

genera – *Homethes*, *Quammenis* Erwin, and *Stenocheila* (Figs 3–5) – also exhibit the derived, divided tergite VIII, as do females of *Aeolodermus* (not figured).

Conversely, males of taxa consistently assigned to Lachnophorini do not exhibit a divided mediotergite VIII (Figs 19–25). These include the American genera *Euceraerus* LeConte, *Anchonoderus* Reiche, *Euphorticus* G. Horn, *Lachnophorus* Dejean, *Calybe* Laporte, and *Calophaena* Klug, and the widespread Old World *Selina* Motschulsky. The spiracle of segment VIII is not associated with the lateral margin of the tergite in these taxa, instead being situated more ventrally in the intersegmental membrane. Therefore the abdominal configuration of taxa assigned to either Odacanthini or Lachnophorini based on abdominal configuration are consistent with results of the DNA-sequence data.



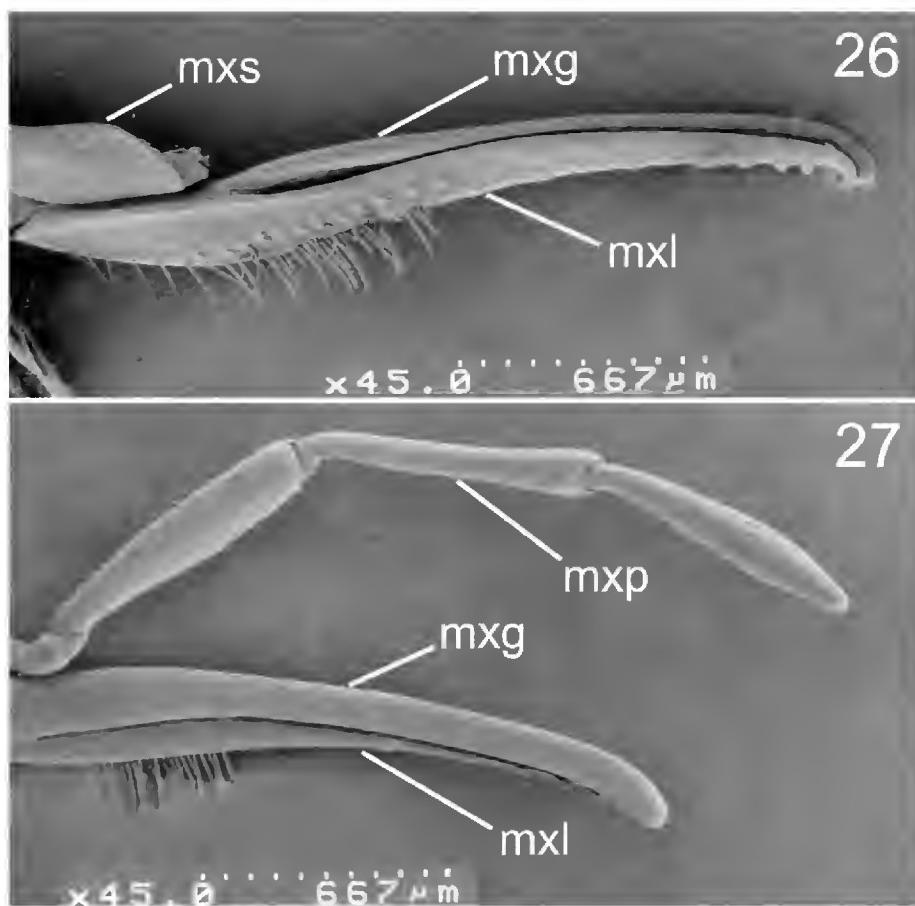
Figures 14–25. 14–18 Male aedeagus with associated abdominal segments VIII and IX, dorsal view for taxa assigned to Odacanthini (see Suppl. material 1): 14, *Colliuris oglobini*; 15, *Erectocolliuris fairmairei*; 16, *Basistichus micans*; 17, *Archicollieus papua*; 18, *Colliuris ludoviciana*; 19–24 Male aedeagus with associated abdominal segments VIII and IX, dorsal view, for taxa assigned to Lachnophorini (Erwin and Zamorano 2014; repository indicated in parentheses): 19, *Selina westermannii* Motschulsky (BMUL); 20, *Eucaerus* sp. (Trinidad, Simla; CUIC); 21, *Anchonoderus subtilis* Bates (CUIC); 22, *Euphorticus pubescens* (Dejean) (CUIC); 23, *Lachnophorus leucopterus* Chevrolat (CUIC); 24, *Calybe argentina* Brèthes (CUIC). 25. Male aedeagus with associated abdominal segments VIII and IX, dorsal view, for taxon assigned to Calophaenini (Erwin and Zamorano 2014; repository indicated in parentheses): *Calophaena cruciata* Bates (CUIC). For abbreviations see Table 1.

Pertinent to the goal of this survey, *Cyphocoleus* males demonstrate the odacanthine abdominal segment VIII condition, with the mediotergite broadly divided into two laterotergites, and the spiracles incorporated into the lateral portion of the tergites (Figs 28–32).

Based on these results, a reexamination of the homology of the bipartite spermatheca observed in lachnophorine and odacanthine taxa is in order. Within Odacanthini, the spermathecal assembly is based on a well-sclerotized spermathecal basal sclerite (sbs) which attaches the spermathecal assembly to the common oviduct (Fig. 39). The spermatheca itself includes a bulb

that extends from the apex of the spermathecal basal sclerite (termed the spermathecal basal bulb by Liebherr and Will 1998), with the duct of the spermathecal gland duct entering at the apex of this bulb. In many Odacanthini, there is also a balloon-like spermathecal apical bulb which joins the spermathecal basal sclerite near the base of the basal bulb (Liebherr and Will 1998). This bulb has no associated ductules or ducts (e.g. Fig. 39) and is connected to the spermathecal basal sclerite by a narrow duct.

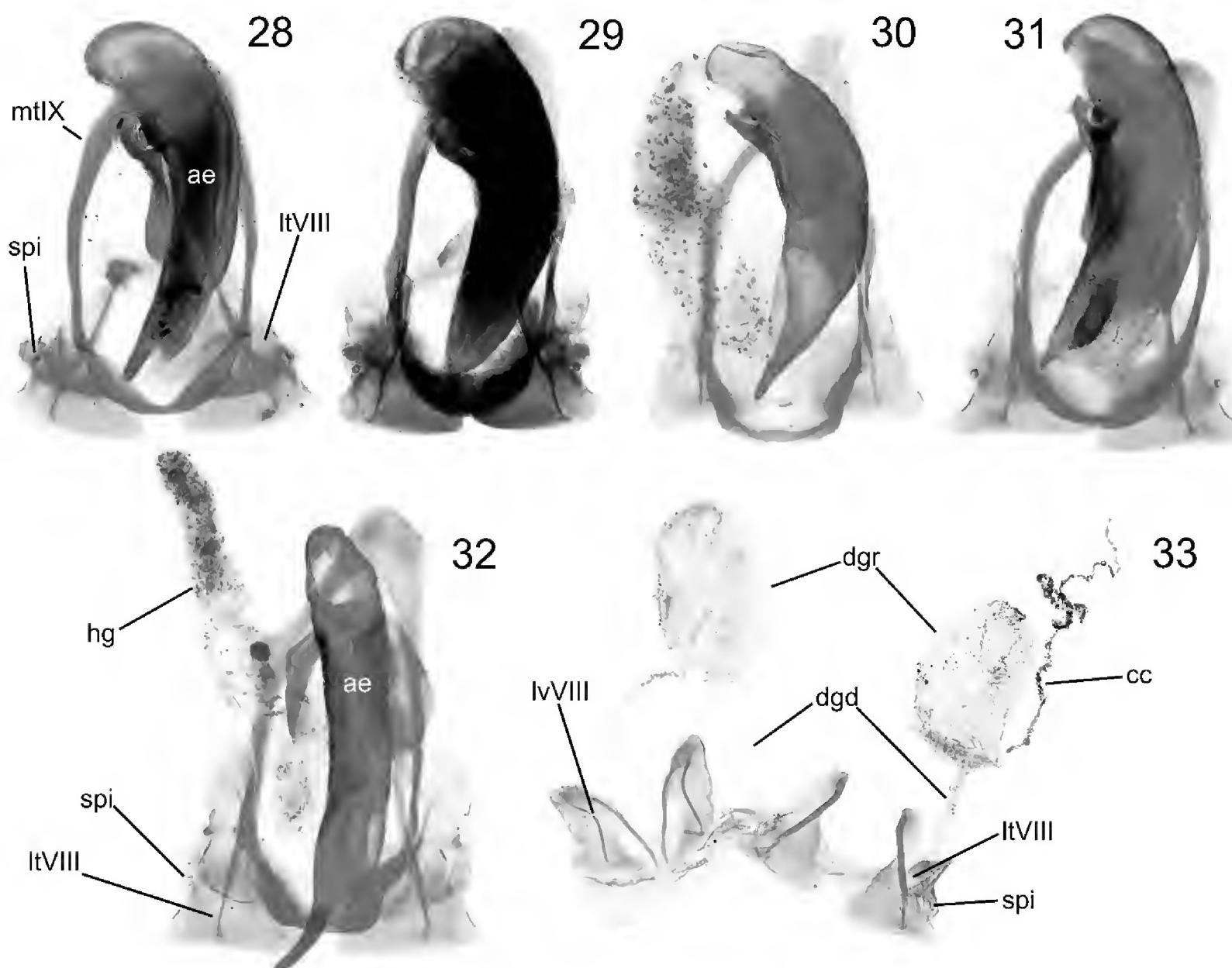
The spermatheca of Lachnophorini does not share this configuration because the spermathecal gland duct joins



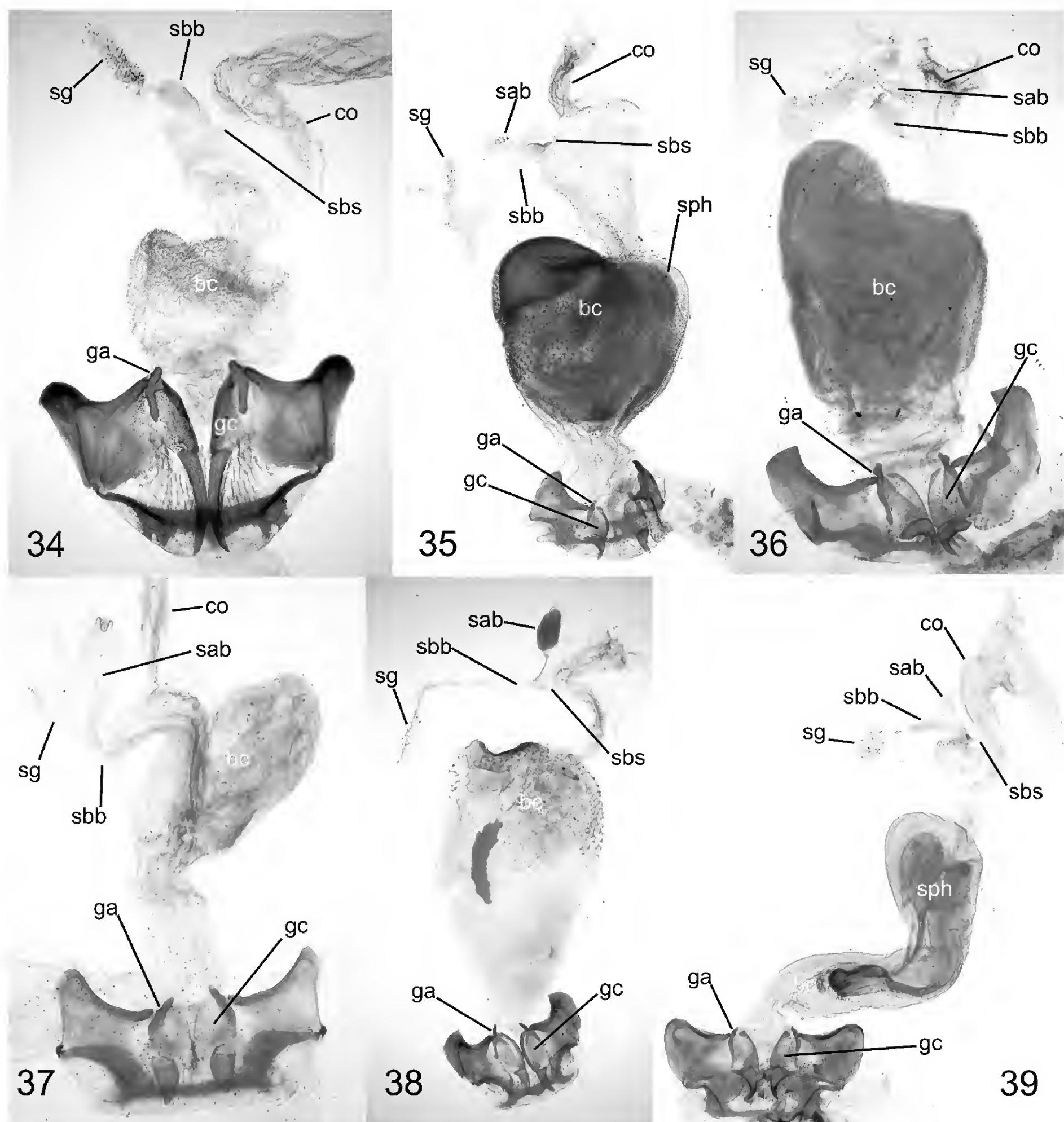
Figures 26–27. Right maxillary stipes, lacinia, galea, and palp, *Cyphocoleus subulatus*: 26, dorsal view; 27, ventral view. Single-segmented galea of *Cyphocoleus* and other Homethina lies laterad the lacinia, with a rabbeted groove on the dorsomedial surface of the galea accommodating the lateral margin of the lacinia, thereby supporting lacinia during alternating, rotary movements of the maxillae. For abbreviations see Table 1.

Table 1. Key to abbreviations for morphological structures indicated in figures.

Abbreviation	Structure
ae	male aedeagal median lobe
bc	female bursa copulatrix
cc	collecting canal of defensive gland
co	female common oviduct
dgd	defensive gland duct
dgr	defensive gland reservoir
ga	female gonocoxal apodeme
gc	female gonocoxa
hg	hindgut
lp	left paramere of male aedeagus
ltVIII	laterotergite of abdominal segment VIII
lvVIII	lateroventrite of abdominal segment VIII
mtlIX	mediotergite of abdominal segment IX
mxg	maxillary galea
mxl	maxillary lacinia
mxp	maxillary palp
mxs	maxillary stipes
sab	apical bulb of female spermatheca
sbb	basal bulb of female spermatheca
sbs	female spermathecal basal sclerite
sg	female spermathecal gland
sp	female spermatheca
sph	spermatophore
spi	spiracle



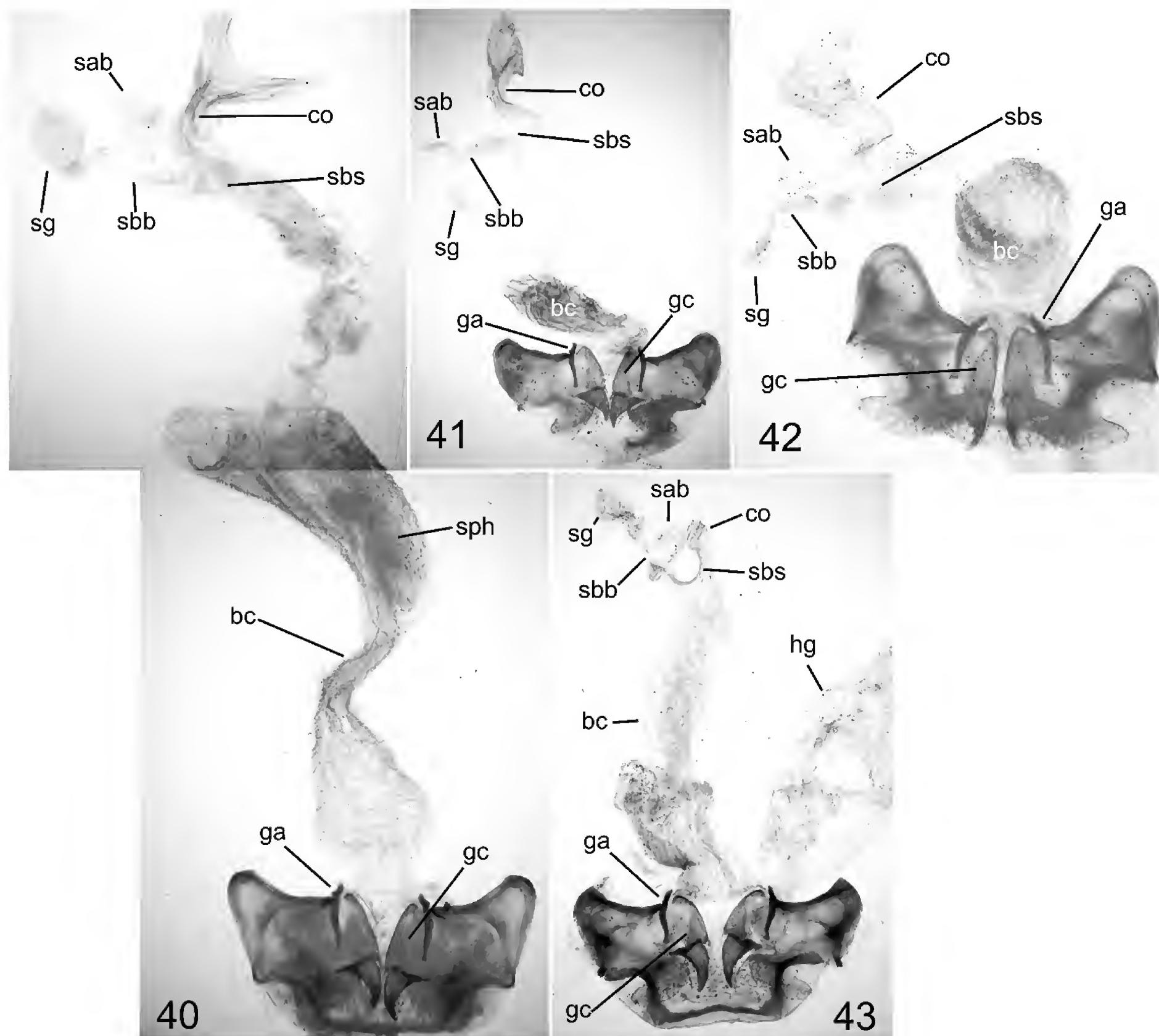
Figures 28–33. 28–32 Male aedeagus with associated abdominal segments VIII and IX, dorsal view, *Cyphocoleus* spp.: 28, *C. heterogenus*; 29, *C. angustatus*; 30, *C. mirabilis*; 31, *C. cordatus*; 32, *C. subulatus*. 33. Abdominal lateroventrites VIII (left) and laterotergites VIII (right), showing membranous division of laterotergites, male *C. latipennis*. Dorsal gland reservoir is globose without dorsal lobe. For abbreviations see Table 1.



Figures 34–39. Female gonocoxal ovipositor and female reproductive tract, ventral view for taxa assigned to Odacanthini (see Suppl. material 1): 34, *Actenonyx bembidioides*; 35, *Homethes gracilis*; 36, *Stenocheila lacordairei*; 37, *Pentagonica daimella*; 38, *Scopodes edwardsii*; 39, *Eudalia atrata*. For abbreviations see Table 1.

the spermatheca near the base of the basal bulb, not at the apex (Liebherr and Will 1998: fig. 55). This fundamentally different entry point for the spermathecal gland duct argues against homology of the basal bulb in Odacanthini versus Lachnophorini. Upsetting that homology undermines the homology of the bipartite spermathecal condition in the two tribes, suggesting the possibility that the bipartite condition evolved twice. This possibility is congruent with both the molecular phylogenetic data (Ober and Maddison 2008) and the results of the survey of abdominal tergite VIII presented above.

In conclusion, the outgroups considered appropriate to include with *Cyphocoleus* in a cladistic analysis include those assigned to Odacanthini and Pentagonalini (Liebherr and Will 1998), plus the additional taxa found to share the divided mediotergite VIII and the odacanthine female reproductive tract with spermathecal gland duct entering the apex of the spermathecal basal bulb (Figs 34–43, Suppl. material 1). Those taxa previously assigned to Lachnophorini (or Lachnophorina and Calophaenina *sensu* Erwin and Zamorano 2014: Figs 19–25) are not included, as they do not form a natural group with Odacanthini as defined



Figures 40–43. Female gonocoxal ovipositor and female reproductive tract, ventral view for taxa assigned to Odacanthini (see Suppl. material 1): 40, *Neoeudalia nigra*; 41, *Odacantha melanura*; 42, *Colliuris ludoviciana*; 43, *Colliuris subdistincta*. For abbreviations see Table 1.

here. It follows that the hypothesis pairing Odacanthini and Lachnophorini as sister groups comprising a supertribe Odacanthitae (Liebherr 1988) must be discarded.

Ingroup phylogenetic analysis. The 79 taxa included in the analysis (Suppl. material 1, Figs 44, 45) were assessed for 119 morphological characters: 112 synapomorphies, 4 symplesiomorphies of the outgroup root taxon, 1 autapomorphy among the ingroup taxa for female characters, with some taxa not codable for females due to absence in the study set, and 2 autapomorphies included for future assessment against additional taxa (Suppl. material 2). The 78-taxon odacanthine ingroup was rooted at *Celaenephes linearis* (Walker) based on inclusion of that taxon in the “Pentagonicini + Odacanthini clade g” (Ober and Maddison 2008: fig. 2). An additional 120th character coding for geographic distributions of the taxa was also included to allow visualization of area relationships among the odacanthine taxa, although this character was not active in the analysis.

Characters. Characters are numbered sequentially starting at the anterior of the head, posterad to the abdomen and then legs for external characters, then to internal anatomical, male genitalic, and female reproductive tract characters. The distribution of character states among taxa can be viewed under the “Diagnoser” toggle of WinClada (Nixon 2002), using the data file provided as Suppl. material 2.

Character 0. Labrum: truncate to slightly emarginate apically (0); broadly convex apically (1).

Character 1. Mandibular length: short, \leq to $\sim 1.5 \times$ distance antenna base-labral margin (0); moderately elongate, $1.5\text{--}1.75 \times$ distance (1); elongate, $>1.8\text{--}2.25 \times$ distance (2) (Fig. 47); very elongate, $>2.3 \times$ distance (3) (Fig. 48).

Character 2. Maxillary galea comprising: two subequal segments (0); a single elongate segment (1) (Figs 26,

- 27). The united, single-segmented galea was observed in individuals of the *Cyphocoleus* spp. described by Chaudoir (1877). He also noted this condition in the genera *Homethes* and *Stenocheila* (Chaudoir 1872).
- Character 3. Maxillary galea: free of the lacinia (0); appressed to the outer surface of lacinia (1) (Fig. 26).
- Character 4. Apical maxillary palpomeres: apparently glabrous (0); covered with short, sparsely distributed setae (1); covered with long, dense setae (2).
- Character 5. Antennal scape: moderately long, length $2.0\text{--}2.3 \times$ breadth (0); elongate, length $2.4\text{--}3.2 \times$ breadth (1) (Fig. 46); very elongate, length $3.5\text{--}4.9 \times$ breadth (2) (Fig. 48).
- Character 6. Antennal scape: gracile to moderately broad, anterior surface at most slightly bowed (0); bowed, swollen, anterior surface distinctly convex (1) (Figs 99–103).
- Character 7. Antennomeres 2–3: glabrous except for apical setae (ring setae on 3) (0); with short setae sparsely distributed along shaft (1); with short setae densely distributed along shaft (2).
- Character 8. Antennomeres: concolorous or basal antennomeres paler (0); apical 3–4 antennomeres distinctly paler, testaceous (1); antennomeres 7–8 or 8–9 paler (2); antennomeres 7–10 paler (3).
- Character 9. Frons: broadly convex (0) (Fig. 47); with broad median convexity and two adjacent paralateral grooves (1) (Fig. 104); with cristate median convexity and paralateral grooves (2) (Fig. 1).
- Character 10. Frons: smooth or irregularly upraised (0); distinctly punctate (1).
- Character 11. Supraorbital setae: two, both anterior and posterior seta present (0); posterior seta present, anterior absent (1); neither anterior nor posterior seta present (2).
- Character 12. Eyes: moderate large, greatly projected (0); hypertrophied, convexly projected (1).
- Character 13. Eye size: moderate (0) (Fig. 82); very small (1) (Fig. 49).
- Character 14. Number of ommatidia across horizontal diameter of eye: 10 or more (0); 8 (1).
- Character 15. Eye convexity: moderately convex (0) (Fig. 50); very convex, pop-eyed (1) (Fig. 47).
- Character 16. Eye convexity: moderately convex (0) (Fig. 99); nearly flat (1) (Fig. 101).
- Character 17. Neck: without any constriction behind vertex, sides not constricted (0) (Fig. 47); with moderate constriction behind vertex, sides constricted (1) (Fig. 48); with very distinct neck constriction, head pedunculate (1) (Fig. 99).
- Character 18. Neck defined by: elongate gena, head stalked (0) (Fig. 47); short gena, head truncate behind (1) (Fig. 99).
- Character 19. Submentum: with two setae each side (0); with single seta (inner) each side (1).
- Character 20. Ventral surface of gena: glabrous (0); with seta each side (1).
- Character 21. Mentum: without median tooth (0); with shallow bidentate tooth (1); with obtuse median tooth, apex rounded (2); with acute median tooth, apex pointed (3).
- Character 22. Suture between mentum and gula/submentum straight and complete (0); reduced to an indistinct impression, straight or not (1).
- Character 23. Suture between mentum and gula/submentum: complete across width, distinct or not (0); absent medially, mentum and gula fused (1).
- Character 24. Pronotum: orbicular (0) (Fig. 47); parallel-sided or basal margins straight and divergent (1) (Figs 48, 49).
- Character 25. Pronotal length: subequal or less than width (0) (Fig. 47); greater than width (1) (Figs 48–49).
- Character 26. Pronotal length: less than to twice pronotal width (0); twice or more than twice pronotal width (1) (Fig. 48).
- Character 27. Front angles: rounded (0) (Fig. 48); briefly protruded (1) (Fig. 47); extensively protruded, acute (2) (Fig. 49); extensively protruded, horn-like or digitiform process (3) (Figs 101–103).
- Character 28. Pronotal hind angles: flat, not upraised (0) (Fig. 47); with slightly upraised tubercle (1) (Fig. 48); with elongate, spinose projection (2) (Fig. 104); with very elongate, horn-like or digitiform process (3) (Figs 101–103).
- Character 29. Median base: bordered by evenly convex marginal bead (0) (Fig. 47); bordered laterally by sinuate bead, basally by straight margin (1) (Figs 48–50).
- Character 30. Pronotal basal margin: straight between pronotal hind angles (0); with median lobe extended posteriorly (1).
- Character 31. Pronotal disc: smooth or punctate laterally (0) (Fig. 47); with shallow transverse wrinkles (1) (Fig. 123); with moderate transverse wrinkles (2) (Fig. 121); with deep transverse wrinkles (3) (Figs 122, 125).
- Character 32. Pronotal disc: smooth or transversely wrinkled overall (0); punctate overall (1).
- Character 33. Pronotal disc: without parasagittal impressions (0) (Fig. 121); with shallow parasagittal impressions (1) (Fig. 122); with deep parasagittal impressions (2) (Fig. 125).
- Character 34. Prothoracic episternum: not expanded nor visible in dorsal view (0) (Fig. 47); expanded, outer surface visible in dorsal view (1) (Fig. 99).
- Character 35. Proepisternum: smooth, impunctate (0); punctured in posterior half (1); distinctly punctured or wrinkled over entire surface (2).
- Character 36 (unordered). Pronotal lateral seta: present (0); absent (1); more than one seta present (2).
- Character 37 (unordered). Pronotal basal seta: present (0); absent (1); more than one seta present each side (2).
- Character 38. Pronotal base: smooth, wrinkled or punctate as anterior portion (0); punctate (1).
- Character 39. Pronotal lateral margin: straight to convexly curved (0); angulate at lateral seta (1).
- Character 40. Pronotal lateral margin: ridge-like, lateral depression present (0); absent, lateral seta if present not in groove (1).
- Character 41. Elytral humerus: sinuously rounded laterad parascutellar striole (0) (Fig. 164); tightly rounded to angulate near or laterad base of fifth interval (1) (Fig.

- 161); distinctly angulate near or laterad base of fifth interval (2) (Fig. 49).
- Character 42. Elytral humerus: broadly extended laterally (0) (Fig. 47); narrowly extended laterally (1) (Fig. 48); very narrowly extended laterally (2) (Fig. 84).
- Character 43. Elytral basal margin: straight between humeri across scutellar base (0) (Fig. 49); inflexed at scutellar base, elytral base cordate (1) (Fig. 47).
- Character 44. Elytral basal groove: of uniform depth from scutellum to humerus (0); with deep pit at base of stria 3 (2).
- Character 45. Elytral lateral marginal depression: narrow outside anterior series of lateral elytral setae (0) (Fig. 47); broadly expanded outside anterior series of lateral elytral setae (1) (Fig. 49).
- Character 46. Elytral lateral margin: convex laterad anterior series of lateral elytral setae (0) (Fig. 47); invaginated laterad anterior series of lateral elytral setae (1) (Figs 48, 49).
- Character 47. Parascutellar seta: present, doubled or not (0); absent (1).
- Character 48. Parascutellar seta: in articulatory socket nearly to coplanar with interval 1 (0); in papillate articulatory socket elevated above interval 1 (1).
- Character 49. Parascutellar seta: single each elytron (0); double each elytron (1).
- Character 50. Dorsal elytral setae: 3–4 or more (0); 2 (anterior and medial setae present) (1); 1 (medial only) (2); 0 (3).
- Character 51. Dorsal elytral setae: 3–4 or less (0); more than 3–4, present along length of interval 3 (1).
- Character 52. Dorsal elytral setae: articulatory socket coplanar with elytral disc (0); set in foveate articulatory socket (1).
- Character 53. Dorsal elytral setae: not surrounded by differentially colored cuticular spot (0); surrounded by differentially colored cuticular spot (1).
- Character 54. Elytral macrosetae: present only on interval 3 (0); also present on interval 5 (1); also present on intervals 5 and 7 (2); also present in intervals 1, 5 and 7 (3); present on all intervals 1–7 (4).
- Character 55. Elytra: evenly convex from base to apex (0); with shallow lateral depression at basal 1/3 of length (1); with deep, distinct lateral depression at basal 1/3 of length (2); with deep lateral depressions in basal and apical halves (3).
- Character 56. Discal elytral intervals: flat to slightly convex (0); moderately convex (1); very convex (2) (Figs 47–50).
- Character 57. Elytral striae: present, shallow to deep (0); present basally and laterally, absent in apical half (1); absent (2).
- Character 58. Elytral intervals 3, 5, and 7: of equal convexity (or nearly equal) to others on disc (0) (Fig. 47); broader and more elevated than intervals 1, 2, 4, and 6 (1) (Fig. 48).
- Character 59. Elytral striae: impunctate to minutely punctate (0) (Fig. 47); regularly punctate (1) (Fig. 101); distinctly, broadly and deeply punctate (2) (Fig. 99).
- Character 60. Lateral elytral setae: with articulatory sockets not greatly raised (0); with papillate articulatory sockets (1).
- Character 61. Elytral apices: meeting at suture, margins evenly curved (0) (Figs 161–164); separately rounded with space between elytra (1) (Fig. 99); separately pointed, elytra bispinose apically (2) (Fig. 101); separately spinose, each elytron with apical spine (3).
- Character 62. Elytral subapical spine at apex of stria 3: absent (0); present (1).
- Character 63. Subapical sinuation: nearly obsolete, elytral apices obliquely truncate (0); evident (1); very distinct, angularly concave (2); very distinct, with subapical spine laterally (3).
- Character 64. Apical elytral setae: subapical and apical present (0); only subapical present (1).
- Character 65. Mesepisternal fovea: absent (0); present (1).
- Character 66. Metathoracic flight wings: present, functional with folded apex (1); vestigial (2).
- Character 67. Metepisternal length to width ratio: 2.5–4.0 (0); 2.0–2.4 (1); 1.3–1.6 (2); less than or equal to 1.0 (3).
- Character 68. Abdominal-metathoracic juncture: loosely articulated, membranous (0); tightly articulated, fused (1).
- Character 69. Elytral and abdominal ventrite cuticle: moderately sclerotized, somewhat flexible (0); extremely thick and brittle (1).
- Character 70. Surface of frons: apparently glabrous, micropunctures may be present (1); with short, sparse pelage (2); with dense pelage of visible setae (3).
- Character 71. Elytral intervals: glabrous except for primary setae (micropunctures possible) (0); with very short pelage of secondary setae (1); with moderately short pelage of secondary setae (2); with long dense pelage distributed over surface (3).
- Character 72. Dorsal pelage setae: fine, thin, pointed (0); thick, club-like (1) (Figs 101–103).
- Character 73. Head surface: glabrous except for macrosetae (0); with additional macrosetae posterad supraorbital setae (1).
- Character 74. Frons microsculpture: evident, isodiametric to transverse (0); reduced, not traceable except in spots (1); absent (2).
- Character 75. Frons: covered with distinct isodiametric sculpticells (0); covered with evident, stretched isodiametric sculpticells (1); covered with dense transverse microsculpture (1).
- Character 76. Frons surface: smooth (0); with longitudinal microreticulations (1).
- Character 77. Pronotal disc: with regular isodiametric mesh (0); with evident transverse microsculpture (1); with fine transverse lines (2); glossy, without evident microsculpture (3).
- Character 78. Pronotal discal surface: without microcuticular patterns (0); with swirling microcuticular ridges (1).
- Character 79. Elytral disc microsculpture: isodiametric mesh, may be in transverse rows (0); transverse mesh (1); evident transverse lines (2); not evident, surface glossy (3).

- Character 80. Elytral microsculpture sculpticells: moderately raised to not raised (0); extensively raised into granulate microsculpture (1).
- Character 81. Elytral disc: without window-like ivory spots (0); with apical window-like spot each elytron (1); with apical and basal window-like spot each elytron (2).
- Character 82. Environmental patina: absent (0) (Figs 47–50, 82–84); present (1) (Figs 85, 102).
- Character 83. Male abdominal apical setae: 2 (1 on each side) (0); 4 (2(rarely 3) on each side) (1); 8 (4 on each side) (2).
- Character 84. Female apical abdominal setae: 4 or more (2 or more each side) (0); 2 (1 each side) (1).
- Character 85. Apical visible male abdominal ventrite medially: convex to slightly, broadly concave (0); with distinct, deeper notch-like invagination (1).
- Character 86. Metacoxae: trisetose (0); bisetose (1). A trisetose metacoxa has two lateral setae and one closer to body midline. The bisetose condition includes only the two lateral setae.
- Character 87. Femora: moderately elongate (0) (Fig. 47); extremely elongate (1) (Fig. 48).
- Character 88. Femora: concolorous from base to apex (0) (Fig. 47); with distinct, paler band in apical half, knees dark as base (1) (Fig. 104); with apex dark, basal 1/2 – 4/5 pale (2).
- Character 89. Fourth metatarsomere: truncate apically, without lateral lobes or with lobes short, obtuse (0) (Fig. 49); lobate, apical lobes half as long but shorter than mid-dorsal length (1) (Fig. 85); lobate, apical lobes longer than mid-dorsal length (2) (Fig. 99, 104).
- Character 90. Dorsal surface of tarsomeres: setose, setae long (0); sparsely covered with short setae (1); glabrous (2).
- Character 91. Metatarsomere 5: with 2 rows of 6–8 long ventrolateral setae (0); with 2 rows of 4–5 long ventrolateral setae (1); with 2 rows of 3–(2) long ventrolateral setae (3); with two rows of 3 short ventrolateral setae (4).
- Character 92. Abdominal tergite 8: complete, undivided medially by membranous cuticle (0); divided medially by narrowly membranous cuticle (1); divided medially by broadly membranous cuticle (2); divided medially by broad membrane, laterally extended as flaps (3).
- Character 93. Male tergite VIII apodemes: narrow, the laterotergite stalked (0); broadly triangular, therefore the laterotergite triangular (1).
- Character 94. Abdominal tergite 8 sclerotized margin: not incorporating spiracle (0); with spiracle incorporated (1).
- Character 95. Male tergite IX ring sclerite: angulate apically, wishbone-shaped (0); hemicircular apically, horseshoe shaped (1).
- Character 96. Male aedeagal median lobe: gracile (0) (Fig. 154); robust, broad dorsoventrally (1) (Fig. 153).
- Character 97. Aedeagal median lobe: short to elongate but broader basally than toward apex (0); elongate, dorsal and ventral surfaces parallel for much of length (1).
- Character 98. Aedeagal median lobe apex: gradually narrowed apicad ostium (0); parallel-sided, elongate apicad ostium (1); parallel-sided basally, curved into a hook apically (2).
- Character 99. Male aedeagal median lobe apex: evenly attenuated or expanded (0) (Fig. 154); sinuously curved ventrally, the apex offset to shaft (1) (Figs 91–98).
- Character 100. Male aedeagal median lobe apex: of moderate length, attenuate or spoon-shaped (0) (Figs 141–154); exceedingly elongate, porrect (1) (Figs 155–160).
- Character 101. Male aedeagal median lobe apex: attenuated, evenly or not, but tip acuminate (0) (Fig. 53); moderately broad, tip rounded (1) (Fig. 57); broadly rounded, spoon-shaped (2) (Fig. 55); broader apically with basal constriction, spatula-shaped (3) (Fig. 87).
- Character 102 (unordered). Male aedeagal internal sac: evenly spiculated (0) (Fig. 54); with ventral sclerotized field or tooth (1) (Figs 58, 59); with apical cockscomb of macrospicules (2) (Figs 56, 87); with apical tooth-like projection (3) (Fig. 86).
- Character 103. Female abdominal tergite IX: broadly convex (0); narrowly convex, apex tightly rounded (1).
- Character 104. Female abdominal tergum X: broad, broadly extended laterally beyond gonocoxites (0); narrow, little extended beyond gonocoxites (1).
- Character 105. Female bursa copulatrix: membranous (0) (Figs 60, 61); sclerotized across surface but translucent (1) (Fig. 64); heavily sclerotized, opaque (2) (Fig. 65).
- Character 106. Female bursa copulatrix: membranous, inner surface smooth (0); sparsely covered with spicules on inner surface (1); densely covered with thin or thick spicules on inner surface (2).
- Character 107. Female bursa copulatrix: vase-like, common oviduct short basad spermatheca (0); basally broad, with elongate oviduct basad spermatheca (1); basally broad, rectum-like, with very elongate extension to sp (2).
- Character 108. Female spermathecal assembly: without apical bulb basally adjoining basal bulb (0); with apical bulb entering basad basal bulb (1).
- Character 109. Spermathecal basal bulb: broadly joined to spermathecal sclerite (0); narrowly joined by a duct to spermathecal sclerite (1).
- Character 110. Spermathecal gland reservoir: globose or elongate, not divided apically (0); linear, divided or not apically, ductules on elongate strand (1).
- Character 111. Basal gonocoxite 1: with 1–3 apical fringe setae (0); with 5–12 apical fringe setae (1); with 14–16 apical fringe setae (2).
- Character 112. Basal gonocoxite 1: not extended medially mesad inner margin of gonocoxite 2 (0); convexly extended medially mesad inner margin of gonocoxite 2 (1).
- Character 113. Basal gonocoxite 1 basolateral apodeme: gradually thinned apically (0); very thick throughout length, bar-like (1).
- Character 114. Apical gonocoxite 2: with 2 (or 1) lateral ensiform setae (0) (Fig. 66); with 3 lateral ensiform setae (1) (Fig. 67); with 4–5 lateral ensiform setae (2).

- Character 115. Lateral ensiform setae: arrayed along lateral margin of apical gonocoxite 2 (0); grouped near apex of apical gonocoxite 2 (1).
- Character 116. Apical gonocoxite 2: acuminate apically (0); triangular, rounded apically (2).
- Character 117. Gonocoxite 2: much narrower basally than length, falciform (0); narrower basally than width, acuminate to triangular (1).
- Character 118. Dorsal ensiform seta of gonocoxite 2: present (0); absent (1).
- Character 119 (inactive). Zoogeographic Region: New Caledonia, New Zealand, Australia, Asia, Africa incl. Madagascar, Palaearctic, Neotropical, Nearctic.

Cladistic analysis. The 79 taxon × 119 character matrix was developed in WinClada (Nixon 2002) and analyzed under parsimony (Goloboff 1999) using the ratchet (Nixon 1999). An initial analysis using 200 ratchet runs followed by a bout based on 10,000 ratchet runs resulted in the same set of 29 equally parsimonious trees (step length 835, CI = 22, RI = 74). The strict consensus of the 29 trees collapsed eight nodes (Fig. 44), resulting in a consensus tree of 852-step length. The majority rule consensus tree collapsed the same eight nodes, leaving all remaining resolved nodes at 100% tree support (Fig. 45). The data set (Suppl. material 2) was submitted to TNT – Tree Analysis using New Technology (Goloboff and Catalano 2016) – using the New Technology search option, with 12 initial add-sequences, and 20 findings of minimum length, in order to confirm the 835-step minimum length cladogram. The TNT program examined 466,964,990 rearrangements, finding a minimum length 835-step tree 20 times.

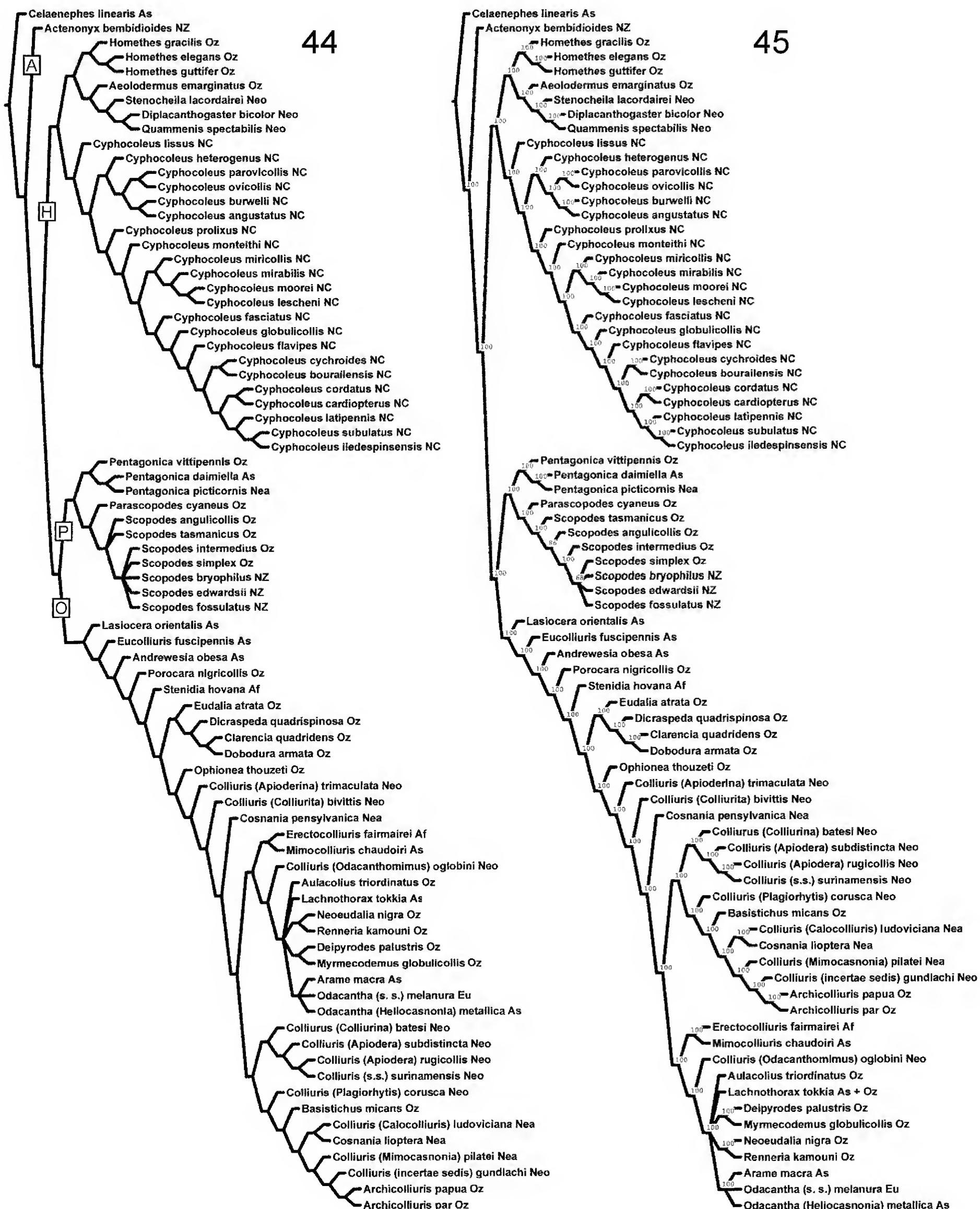
Classification of Odacanthini stat. n. The tribe Odacanthini is hereby proposed to consist of four monophyletic subtribes: **1**, Actenonyicina; **2**, Homethina subtrib. n. (type genus *Homethes* Newman); **3**, Pentagonicina; and **4**, Odacanthina (Fig. 44, Suppl. material 1). Relative to the *Celaenephes linearis* outgroup, monophyly of Odacanthini is supported by nine characters. Three unreversed synapomorphies of the tribe are the medially membranous abdominal tergite VIII (character 92, state 1), the incorporation of the abdominal VIII spiracles into the lateral margin of the laterotergites (character 94, state 1: Figs 2–18, 28–33), and spermathecal basal bulb joined to common oviduct by narrow, sclerotized spermathecal basal sclerite (character 109, state 1). Other characters supporting the basal node defining Odacanthini are subordinately reversed on the tree. One such as the absence of the basal pronotal seta (character 37, state 1) is shared by most odacanthine taxa, however the character is reversed, i.e. seta present, among *Parascopodes* Darlington and most *Scopodes* in the analysis. Moreover some Odacanthina have more than one seta present near the pronotal hind angle (e.g., *Odacantha* and *Arame*). Also, the metacoxae are bisetose (character 86, state 1) in all odacanthines in the analysis with the exceptions of *Cyphocoleus angustatus*, *Dicraspeda quadrispinosa*, and species

of *Aulacolius*, *Lachnothorax*, *Arame*, and *Odacantha*. Odacanthines generally have moderately elongate to very elongate mandibles (character 1, states 1–3), but this is reversed to short mandibles in *Homethes*, *Aeolodermus*, the pentagonicines, and the species of *Ophionea* and *Myrmecodemus* in the Odacanthina. More numerous and complex patterns of reversals from the derived state occur in the final 3 characters supporting the basal odacanthine node: **1**, mentum with shallow bidentate tooth (character 21, state 1); **2**, subapical elytral sinuation evident (character 63, state 1); and **3**, male aedeagal median lobe broad dorsoventrally (character 96, state 1), so these characters cannot be used to diagnosis the tribe.

Actenonyicina. The genus *Actenonyx* is included within Odacanthini based on the shared-derived abdominal configuration (Fig. 2), and the presence of a spermathecal basal sclerite (Fig. 34). However the absence of an apical bulb in the spermathecal assembly (character 108, state 1: e.g. Fig. 35) supports placement of *Actenonyx* as the adelphotaxon to the rest of the Odacanthini (Fig. 44, lineage A). This placement is supported also by the extremely narrow and stiletto-like gonocoxae (character 117, state 0: Fig. 34) compared to the broader gonocoaxal configuration observed in females throughout the rest of the tribe (character 117, state 1: e.g. Figs 35–39). The genus can be diagnosed by the following combination: **1**, antennomeres 2–3 glabrous (character 7, state 0); **2**, gena with a ventral seta present (character 20, state 1); **3**, pronotal disc with shallow transverse wrinkles (character 31, state 1); **4**, pronotal lateral seta absent (character 36, state 1); **5** apical tarsomere with reduced ventral setation, only 3 short ventrolateral setae each side (character 91, state 3); and **6**, male aedeagal median lobe evenly narrowed apically (character 101, state 0: Fig. 2).

Homethina + *Pentagonicina* + *Odacanthina*. The presence of the spermathecal apical bulb and broader gonocoxae (characters 108, 117) are synapomorphies of this clade that excludes *Actenonyx*. The antennae are nearly uniformly elongate (character 5, states 1 and 2), and the apices of the elytra are generally separately rounded each side of the suture (character 61, state 1), though this condition is reversed in some *Cyphocoleus*, *Aeolodermus emarginatus*, and several species within Pentagonicina and Odacanthina.

Homethina subtrib. n. This subtribe is dramatically supported by the one segmented maxillary galea (character 2, state 1) that is appressed to the outer margin of the lacinia (character 3, state 1: Figs 26, 27). Although the state distributions for these two characters are identical in this analysis, a single-segmented maxillary galea is observed also in *Amerizus*, though in this taxon the galea is apically free of the lacinia, justifying the separation of these two attributes into distinct characters here. The mentum lacks a median tooth (character 21, state 0), a state shared with *Pentagonica* and some *Scopodes* spp. The humeri are tightly rounded to angulate (character 41, state 1: Figs 47–50) throughout the early-diverging lineages of this subtribe, although this condition is reversed



Figures 44–45. Parsimony cladograms comprising exemplar taxa of Odacanthini used in phylogenetic analysis, rooted at the out-group *Celaenephes linearis* (tribe Lebiini): **44**, 852-step length strict consensus of 29 equally parsimonious trees of 835-step length (CI = 22, RI = 74) [A = subtribe Actenonyicina; H = subtribe Homethina subtrib. n.; P = subtribe Pentagonalicina; O = subtribe Odacanthina]; **45**, majority-rule consensus of 29 equally parsimonious trees with all resolved nodes present in 100% of the multiple equally parsimonious trees; i.e. the majority-rule consensus is the result of collapsing 8 nodes. Abbreviations for geographical distributions include: Af, Africa; As, Asia; Eu, Europe; NC, New Caledonia; Nea, Nearctic; Neo, Neotropical; NZ, New Zealand; Oz, Australia.

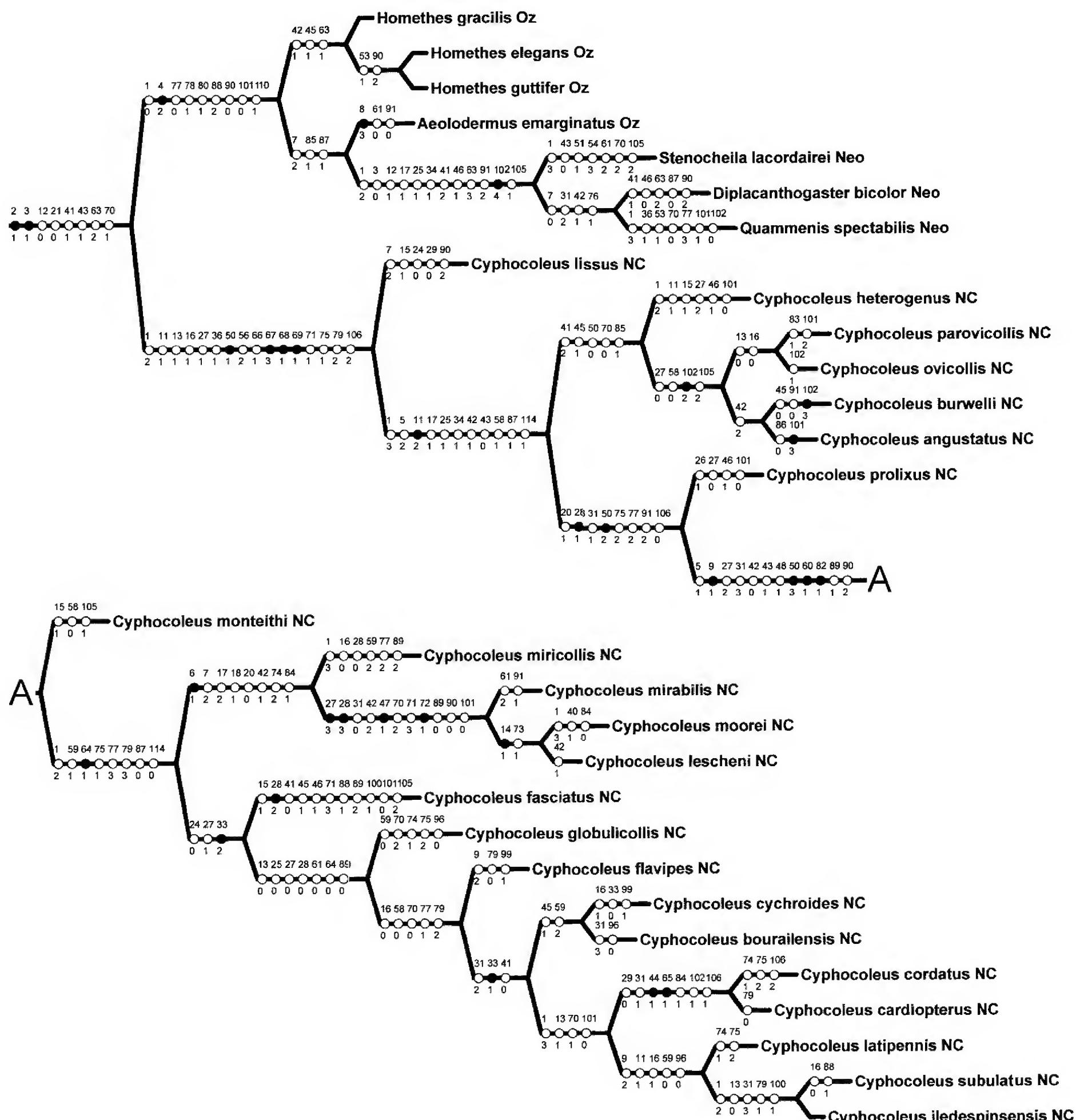


Figure 46. Parsimony cladogram of subtribe Homethina with characters indicated; character numbers above cladogram stems, state numbers below stems [cladogram divided into two parts joined at “A”]; geographic abbreviations as in Figs 44–45.

in homethine taxa with broad elytra (Figs 161–164). Also, the elytra basal margin is inflexed near the scutellum (character 41, state 1) in most taxa (Fig. 27), though also reversed in taxa characterized by narrow bodies (Figs 48–50). Most homethines bear a dense pelage of short to elongate microsetae over various parts of the body (e.g., the frons: character 70). These pelage setae culminate in the dramatically club-shaped setae of *Cyphocoleus mirabilis* and associates (Figs 101–103). This pelage may be reduced to inappreciability in some *Cyphocoleus* spp., but careful examination in side view demonstrates that homethine cuticle is coated with microsetae (noted for *Aeolodermus* by Erwin and Zamorano 2014).

The Homethina divide into two sister clades: *Cyphocoleus* versus five other genera (Fig. 46). These five include: *Homethes* and *Aeolodermus*, both from Australia with the former also represented in Java and the Philippine Islands (Louwerens 1952), the South American *Stenocheila* and *Diplacanthogaster*, and *Quammenis* of Costa Rica. These genera are united by several characters related to microsculpture, coloration, and setation. All exhibit a pronotal surface with swirling microreticular ridges (character 78, state 1), and elytra with raised, granulate sculpticells (character 80, state 1). The femora are paler basally with a dark apex (character 88, state 2), and the apical maxillary palpomeres are densely covered with fine setae (character

4, state 2). Also, based on the female reproductive tracts available for study – i.e. *Homethes guttifer*, *H. gracilis*, *Aeolodermus emarginatus*, and *Stenocheila lacordairei* (Figs 35, 36) – the spermathecal gland ramifies into two arms, with the spermathecal gland duct exiting from the middle of those arms. Monophyly of *Cyphocoleus*, conversely, is based on characters representing mandibular elongation, eye modification, setal loss, wing loss, and modification of microsculpture. All *Cyphocoleus* exhibit elongate mandibles (Character 1) to varying degrees (Figs 47–50), whereas the Australian homethine taxa are characterized by shorter mandibles. Longer mandibles have evolved independently in the South and Central American homethines. The eyes (character 13) are reduced in most *Cyphocoleus*, though reversed to moderate size in eight taxa subordinate within the clade. The anterior supraorbital seta (character 11, state 1) is lost in all *Cyphocoleus* spp., and the posterior supraorbital seta (character 11, state 2) is lost during *Cyphocoleus* evolution, being absent in 17 of the 22 species. The prothoracic lateral seta is also lost in all *Cyphocoleus* (character 36), and except for one subordinate clade, the dorsal elytral setae (character 50, states 1, 2, and 3) are reduced in number or completely absent. A number of characters associated with flight wing loss (Darlington 1936) also define *Cyphocoleus*. These include, in addition to the obvious absence of flight wings (character 66): **1**, a very short metepisternum (character 67, state 3); **2**, a very tightly articulated abdomen (character 68); **3**, thick, brittle cuticle; and perhaps in association with thick cuticle, **4**, convex elytral intervals (character 56). Finally, the cuticle of *Cyphocoleus* often bears transverse microsculpture compared to the raised, isodiametric, or swirling microreticulate patterns of the Australian and New World homethines. Such transverse microsculpture is seen to differing degrees on the head (character 75), pronotum (character 77: reflected in Fig. 46 by loss at the base of the *Homethes*-subtended clade), and elytra (character 79).

Pentagonicina + *Odacanthina*. Cladistic support for monophyly of these two subtribes comes from six characters: **1**, neck very constricted (character 17, state 2: reversed in *Porocara* Baehr of Odacanthini); **2**, gena short before constricted neck (character 18, state 1: observed in *Pentagonicina* and *Lasiocera* Dejean of Odacanthina); **3**, elytral subapical sinuation nearly obsolete (character 63, state 0: a condition observed in most pentagonicines and stem odacanthines from *Lasiocera* to *Stenidia* Brullé; **4**, frons without visible microsculpture (character 74, state 1: extensively reversed to present in *Pentagonica*, some *Scopodes* spp., and several Odacanthini); **5**, tarsomeres dorsally glabrous (character 90, state 2: reversed to setose in *Pentagonica*, some *Scopodes*, and several Odacanthini); **6**, and finally, male aedeagal median lobe dorsal and ventral surfaces parallel near ostium, the ostial opening apical not dorsal (Figs 6–18).

Pentagonicina. The three genera placed in this subtribe exhibit numerous synapomorphies, with the rank of the taxon being the sole change in this historically well-recognized group. The labrum is broadly convex (character 0, state 1), covering the dorsal surfaces of the short

mandibles (character 1, state 0). The apical palpomeres are sparsely setose (character 4, state 1), and the mentum/gular suture is reduced laterally or absent altogether (characters 22 and 23, both state 1). These last characters are reversed in *Scopodes tasmanicus* and *Parascopodes cyaneus*. The pronotum bears a basal lobe that extends posterad between the hind angles (character 30, state 1) – again reversed in *Parascopodes* – but the pronotum is consistently angulate laterally (character 39, state 1), hence providing the basis for the taxon name. Deuve (1993) noted that the abdominal tergite VIII is broadly membranous in *Pentagonica* (character 92, state 2), and though this character supports monophyly on the cladogram (Figs 44, 45), the broadly membranous condition is seen among many odacanthines.

Odacanthini. This very diverse, geographically cosmopolitan subtribe exhibits a broad array of characters and body forms, presumably associated with myrmeco-mimetic behavior while individuals are actively foraging. Focusing on the early-diverging lineages *Lasiocera*, *Eucolluris* Liebke, *Andrewesia* Csiki and *Porocara* allows focus on the odacanthine groundplan. Based on this cladistic analysis, the common ancestor of Odacanthini is characterized by: **1**, frons punctate (character 10, state 1); **2**, submentum with two setae each side (character 19, state 0); **3**, mentum with a median tooth (character 21, state 2); **4**, surface of pronotal disc distinctly punctate (character 32, state 1); **5**, elytral striae punctate (character 59, state 1); **6**, frons without microsculpture between punctures, glossy (character 74, state 2); **7**, pronotal disc (between punctures) without microsculpture, glossy (character 77, state 3); **8**, femora with apex dark (character 88, state 2); **9**, male aedeagal median lobe gracile (character 96, state 0: Figs 8, 9); **10**, male aedeagal median lobe with dorsal and ventral surfaces parallel from basal bulb to base of ostial opening (character 97, state 1: Figs 8–18); and **11**, female bursa copulatrix basally broad with common oviduct elongate basad the spermatheca (character 107, state 1: Figs 39–43).

Taxonomic treatment

Odacanthini Laporte, 1834: 40 [sensu n.]

Homethina subtrib. n.

<http://zoobank.org/AEDC73A8-C144-4635-999D-098AEEA7AEE5>

Cyphocoleus Chaudoir 1877: 188

Atongolium Park & Will 2008: 100 (syn. n.)

Type species. *Cyphocoleus heterogenus* Chaudoir 1877 (designated by Bousquet 2002).

Nomenclatural note. When Bousquet (2002) designated the type species for *Cyphocoleus*, he chose the variant spelling *C. heterogenus* (Chaudoir, 1877: 191), not mentioning the alternate spelling of *C. heterogenus* that was published in the same article (Chaudoir 1877:

196). Fauvel (1882) cited the species as *C. heterogenus*, choosing the correct Latin formation of the name, though he did not mention the alternate spelling. Subsequent authors (Fauvel 1903, Csiki 1931, Lorenz 2005) followed Fauvel's (1882) usage of *C. heterogenus* without mention of the "hetorogenus" variant later cited by Bousquet (2002). Having cited both name variants together here – and therefore acting as first reviser under Article 24.2.3 (I.C.Z.N. 1999) – I designate *C. heterogenus* as the correct original spelling for the type species of *Cyphocoleus*.

Diagnosis. Though quite variable in body proportions and appearance (Figs 47–50, 82–85, 99–103, 161–164), the genus *Cyphocoleus* is amply diagnosed from other Odacanthini based on the following combination of characters: **1**, mandibles elongate, their length measured from anterior condyle to tip $>1.8\times$ distance from anterior margin of antennal articulatory socket to anterolateral labral margin; **2**, maxillary galea 1-segmented and appressed to outer margin of lacinia (Figs 26, 27) [synapomorphy of Homethina]; **3**, only posterior supraorbital seta present, or both supraorbital setae absent; **4**, pronotal lateral and basal setae absent [a configuration shared with *Quammenis spectabilis*: Homethina, and *Actenonyx bembidioides*: Actenonyicina]; **5**, discal elytral intervals convex, not flat; **6**, elytral sub-

apical sinuation very distinctly, angularly concave; **7**, metathoracic flight wings vestigial, that configuration associated with a flightlessness syndrome that includes metepisternum broader than long, tightly articulated metathorax and abdomen [those somites functionally fused], elytra fused at the suture, and very thick and brittle cuticle of elytra and abdominal ventrites; **8**, head, prothorax, and elytra with pelage of secondary setae, those setae ranging from very short spike-like microtrichia, to elongate, paddle- or club-shaped setae (Figs 101, 102); and **9**, transverse microsculpture, or the absence of any microsculpture on frons and pronotal disc. In addition, several characters exhibited by *Cyphocoleus* spp. are shared with various other subtribes of Odacanthini. An elongate scape, length $2.4\text{--}4.9\times$ breadth is observed in all Homethina (Fig. 46). The submentum with only the inner seta each side is shared across Actenonyicina, Homethina and Pentagonicina (Fig. 44). The mentum also lacks a median tooth: a character shared with other Homethina, *Pentagonica*, and some *Scopodes* spp. And the proepisternum is smooth, not punctate as observed in many Odacanthina (Fig. 46). Metatarsomeres 1–3 have narrow dorsolateral sulci both sides, and are broadly convex medially. Metatarsomere 4 bears both subapical and apical setae (Habu 1978).

Identification key to adults of *Cyphocoleus* spp. known from New Caledonia

- 1 Elytral striae impunctate; elytral intervals of subequal convexity, although the 5th and 7th intervals may be indistinctly more convex in beetles of some species; body surface always smooth, without varnish-like exudate that may trap environmental debris (Figs 47–50, 82–84) 2
- Elytral striae punctate, either shallowly punctate with punctures elongate and most evident on discal striae 1–5, or distinctly punctate with deep round punctures in all striae; elytral intervals often carinate, especially the 3rd, 5th or 7th intervals; body surface of all mature individuals covered with varnish-like exudate that may trap environmental debris (Figs 85, 99–103, 121–125, 161–164) (teneral individuals may lack this environmental patina) (e.g. Fig. 104) 8
- 2 Head capsule basally constricted posterad gena, neck constricted (Fig. 48–50, 82–84); pronotal lateral marginal bead subangulately joining straight basal margin; body size larger, standardized body length 9.1–13.1 mm 3
- Head capsule broad basally, not constricted behind eyes (Fig. 47); pronotal lateral and basal marginal beads continuous and evenly convex across median base; body size smaller, standardized body length 6.7–8.2 mm 1. *C. lissus* sp. n.
- 3 Pronotum broadest before midlength, pronotal front angles subangulate and slightly protruded (Figs 50, 82–84) to angulate and protruded (Fig. 49); elytral lateral margin not or only slightly expanded outside anterior series of lateral elytral setae, the elytral basal margin evenly rounded laterad humeral angle 4
- Pronotum broadest in basal half, narrowed apically toward very narrow head, pronotal front angles narrowly rounded, not protruded (Fig. 48); elytral lateral margin with distinct lateral expansion outside anterior series of lateral elytral setae, the elytral basal margin nearly straight between bases of striae 6 and 9 2. *C. prolixus* sp. n.
- 4 Pronotal front angles either minutely protruded, subangulate, or not protruded and obtusely rounded (Figs 50, 82–84) 5
- Pronotal front angles extremely protruded, acute (Fig. 49) 3. *C. heterogenus* Chaudoir
- 5 Pronotum broader (Figs 50, 82), MPW/PL = 0.78–0.90; lateral marginal depression broader, area mesad lateral marginal bead depressed 6
- Pronotum narrower (Figs 83, 84), MPW/PL = 0.68–0.77, lateral marginal depression very narrow, discal convexity extended nearly to lateral marginal bead 7
- 6 Eyes more convex, ocular ratio 1.47–1.55 (Fig. 50); apical abdominal ventrite of males with two setae each side; male aedeagus with internal sac bearing an apical "cockscomb" of stout macrotrichia (Fig. 56) 4. *C. parovicollis* sp. n.
- Eyes less convex, ocular ratio 1.41–1.44 (Fig. 82); apical abdominal ventrite of males with one seta each side; male aedeagus with internal sac bearing a large sclerotized tooth at midlength 5. *C. ovicollis* Fauvel
- 7 Elytral basal groove nearly straight, meeting lateral margin at obtusely angled humerus (Fig. 83); elytra piceous with silvery reflection; male aedeagal median lobe with narrowly rounded apex (Fig. 86) 6. *C. burwelli* sp. n.

- Elytral basal groove more distinctly curved laterally to meet lateral marginal bead at anteriorly projected, right-angled humerus (Fig. 84); elytra with violaceous reflection; male aedeagal median lobe with apical knob-like expansion (Fig. 87) 7. *C. angustatus* sp. n.
- 8 Pronotum tubular, distinctly longer than broad, MPW/PL = 0.59–0.83, front angles acute, protruded, or represented by setose, horn-like, digitiform processes that are longer than their diameter (Figs 85, 99–103) 9
- Pronotum more orbicular, MPW/PL = 0.86–1.10, bordered laterally by convex lateral marginal bead that is much more elevated than anterior margin inside front angles; front angles obtuse, not or only slightly protruded (Figs 104, 121–125, 161–164) 13
- 9 Elytra subellipsoid, basal carina recurved anterad to meet lateral margin at angulate humerus (Fig. 99), or humeri very narrowly projected laterally (Figs 101–103); elytral striae 1–9 with large, deep punctures even near apex, though punctures are more widely spaced apically; head capsule orbicular with deep cervical constriction and genae distinctly curved anterad neck 10
- Elytra broadly ellipsoid, disc convex, appearing inflated, humeri broadly rounded (Fig. 85); elytral striae shallowly punctate; head elongate, cervical constriction shallow, genae gradually constricted to neck 8. *C. montiethi* sp. n.
- 10 Pronotal disc smooth each side of median impression; pronotal front and hind angles presented by horn-like, digitiform processes (Figs 101–103); body including digitiform pronotal processes bearing a sparse pelage of very thick, club-shaped setae, these setae longitudinally arrayed on the elytral intervals 11
- Pronotal disc transversely wrinkled each side of median impression; pronotal front angles acute, projection continuously margined by basal and lateral marginal bead (Fig. 99); body surface covered with sparse pelage of very short, fine setae 9. *C. miricollis* Fauvel
- 11 Eyes very small, little convex, 8 ommatidia along maximal horizontal diameter of eye; body size smaller, standardized body length 4.8–5.4 mm 12
- Eyes small but moderately convex, 12 ommatidia along maximal horizontal diameter of eye; body size larger, standardized body length 6.5–7.0 mm 10. *C. mirabilis* (Park & Will)
- 12 Pronotum without lateral marginal expansion between very elongate anterior and posterior digitiform processes (Fig. 102) 11. *C. moorei* (Park & Will)
- Pronotum with elevated lateral marginal expansion between short, nub-like anterior pronotal process and elongate posterior digitiform process (Fig. 103) 12. *C. lescheni* sp. n.
- 13 Body size smaller, standardized body length 4.8–7.5 mm; pronotum much broader apically than basally, APW/BPW= 1.76–4.0 (Figs 121–125, 161–164) 14
- Body size larger, standardized body length 8.1–8.9 mm; pronotal apical width only slightly broader than basal width, APW/BPW = 1.28–1.40 (Fig. 104) 13. *C. fasciatus* sp. n.
- 14 Pronotum continuously bordered laterally and basally by uniformly elevated marginal bead that convexly crosses median base (Figs 121–124); pronotal disc smooth to shallowly wrinkled, the median disc either extended convexly to lateral carina, or delimited laterally by broad, shallow longitudinal impressions that define a broadly planar lateral marginal depression 15
- Pronotal lateral marginal bead sinuously adjoining median basal margin which bears a much less elevated basal bead or no bead at all (Figs 125, 161–164); pronotal disc deeply and distinctly transversely wrinkled, the median disc delimited by distinct longitudinal impressions that may be deep and narrowly incised (Figs 125, 161), or more broadly, more shallowly, and more irregularly incised (Figs 162–164) 18
- 15 Pronotal disc distinctly wrinkled transversely, wrinkles extended nearly to lateral carina, lateral longitudinal impressions indistinct, broad and shallow (Figs 121, 122); elytra ellipsoid, maximum breadth only slightly anterad midlength 16
- Pronotal disc smoother, transverse wrinkles very shallow to obsolete, median disc delimited by distinct longitudinal impressions that define broadly planar lateral depressions (Figs 123, 124); elytra cordiform, maximum breadth distinctly anterad midlength, the posterior half distinctly tapered to the narrow apex 17
- 16 Elytral margin broadly extended laterally outside anterior series of lateral elytral setae, the basal margin distinctly, sinuously recurved anterad parascutellar seta, humeri broadly protruded anteriorly (Fig. 121); supraorbital setae absent, vertex glabrous mesad compound eyes; pronotal disc lacking distinct longitudinal parasagittal impressions, the transverse wrinkles extended evenly or nearly evenly to lateral marginal bead 14. *C. cychroides* Chaudoir
- Elytral margin only narrowly extended laterally outside anterior series of lateral elytral setae, the setae close to lateral marginal bead; elytral basal margin only slightly recurved, the broadly rounded humeri little protruded anteriorly (Fig. 122); posterior supraorbital seta present each side near hind margin of vertex; pronotal disc with broad, shallow longitudinal parasagittal impressions that interrupt transverse wrinkles and define a broad depression mesad lateral marginal bead 15. *C. latipennis* Fauvel
- 17 Eyes small in diameter but very convex, appearing “popeyed” (Fig. 123); internal sac of male aedeagal median lobe with large, ventral tooth-like projection incorporating densely packed macrospicules (Fig. 135) 16. *C. cordatus* sp. n.
- Eyes small in diameter but little protruded, outer surface little convex (Fig. 124); internal sac of male aedeagal median lobe with diffuse, little sclerotized ventral projection incorporating numerous macrospicules (Fig. 136) 17. *C. cardiopterus* Chaudoir

- 18 Pronotal and elytral surface with evident microsculpture, the sculpticells isodiametric to transverse resulting in a matte to subiridescent surface; elytra and ventral body surface glabrous except for macrosetae, vertex glabrous to sparsely covered by a few short setae (environmental patina may need to be removed from elytra to assess this character) (Figs 161–164) 19
- Cuticle of pronotum and elytra extremely glossy, surface microsculpture not traceable; body surface with well-developed pelage of microsetae, extremely dense and extremely evident on frons, elytra, and proepisterna (Fig. 125) 18. *C. globulicollis* Fauvel
- 19 Elytral striae deeply and distinctly punctate, their punctures expanding striae breadth (Figs 161, 162); 20
- Elytral striae punctate but punctures shallow and not expanding striae breadth (Figs 163, 164) 21
- 20 Pronotal median discal convexity delimited by deeply incised parasagittal impressions, the pronotal surface smooth, convex between parasagittal impressions and lateral marginal bead (Fig. 161); male aedeagal median lobe short, robust, with broad recurved tip (Fig. 153) 19. *C. flavipes* Fauvel
- Pronotal median discal convexity bordered laterally by broad, shallow parasagittal impressions, transverse wrinkles of disc extended across impressions to reach lateral margin (Fig. 162); male aedeagal median lobe gracile, elongate, shaft expanded slightly at midlength, apex evenly downturned to narrowly rounded tip (Fig. 154) 20. *C. bourailensis* sp. n.
- 21 Legs and antennal scape flavous, distinctly contrasted to piceous body (Fig. 163); apex of male aedeagal median lobe curved dorsally relative to broad shaft, ostium opening on ventral surface of shaft apex (Fig. 155–158) 21. *C. subulatus* sp. n.
- Legs and antennal scape fuscous, only slightly paler than piceous body (Fig. 164), tibiae and tarsi only slightly paler, brunneous; apex of male aedeagal median lobe porrect relative to evenly narrowed shaft, ostium opening on left-ventral surface of shaft apex (Figs 159–160) 22. *C. iledespinsensis* sp. n.

1. *Cyphocoleus lissus* sp. n.

<http://zoobank.org/83EFACA6-BFD1-4FF2-83B5-2A11764976AB>

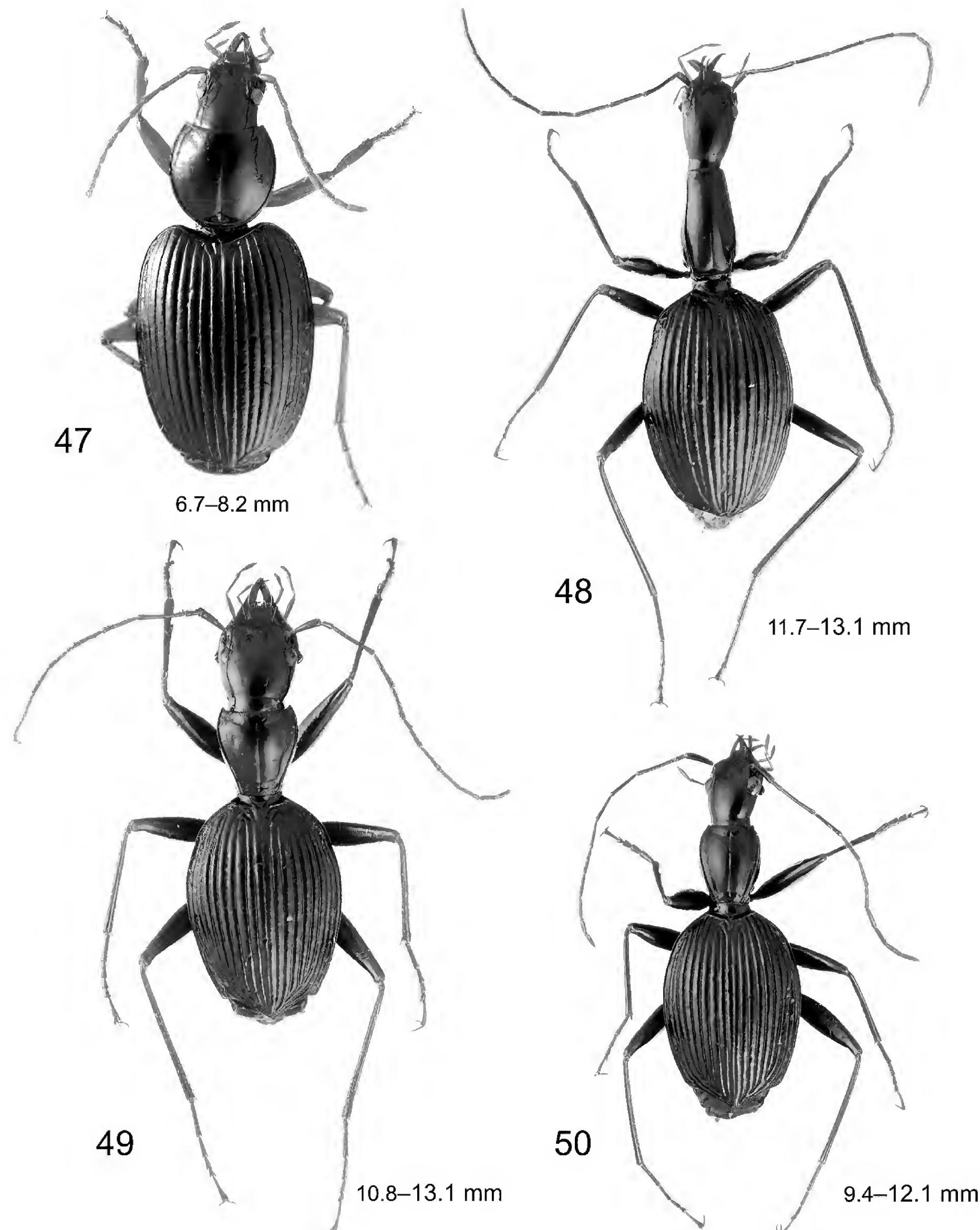
Figures 47, 51, 60, 66, 76

Diagnosis. Dorsal body surface smooth, glossy, with cyanotic iridescent reflection on elytral disc due to dense transverse microsculpture, antennae and legs contrastedly pale than dark body; head stout, broadest at juncture with prothorax, eyes small in diameter with outer surface extremely convex (Fig. 47), 16 ommatidia across horizontal diameter of eye; only posterior supraorbital seta present each side, anterior seta absent; pronotal disc extremely smooth, the lateral marginal bead convexly continuous across the median base in an even arc; elytral humeri broadly rounded, the humerus anterad the depressed scutellum; elytra with anterior and medial dorsal elytral setae, the posterior seta absent; standardized body length 6.7–8.2 mm.

Description (n = 5). Head capsule stout, frons broadly convex, the frontal grooves irregularly doubled anteriorly near clypeus; mandible length 2.0–2.1× distance from anterior margin of antennal articulatory socket to anterolateral margin of labrum; antennae filiform, moderately elongate, scape length 2.55× maximal breadth; eyes convex, but ocular ratio low due to very broad frons, MHW/mFW = 1.42–1.48; subgena without fixed macroseta. Pronotum orbicular, hind angles completely untraceable due to evenly convex lateral and basal margin; front angles briefly protruded; notum only slightly wider than long, MPW/PL = 1.03–1.07; median longitudinal impression shallow, finely incised on disc, terminated basally in a well-defined dimple; anterior transverse impression traceable as obsolete impressed line, anterior convexity flat; proepisternum not visible from above; prosternal process convex anteriorly, with deep median groove on ventral surface that continues onto posterior face. Elytral disc moderately convex,

moderately broad, MEW/EL = 0.71–0.78; elytral intervals moderately and subequally convex across disc; striae indistinctly punctate to smooth, deep and well defined throughout length and in association with lateral elytral intervals; parascutellar seta present, articulatory socket not upraised; lateral elytral setae arranged as (5)6 + 1 + 7(8), the setal articulatory sockets not upraised above surface; both apical and subapical setae present; subapical sinuation moderately incised, convexly meeting lateral margin; apical margins of fused elytra rounded, the elytral apices slightly separated by curvature at suture. Mesepisternum smooth; metepisternum shorter than broad, dorsal length/diagonal width 0.80. Legs of moderate length, mt1 length/tibial length = 0.26; metacoxae bisetose; dorsal surfaces of tarsomeres with two dorsolateral rows of elongate setae; mt4 length to apex of outer lobe 1.6× median length, 3–4 ventrolateral setae each side. Abdomen with apical margin of apical ventrite broadly and very shallowly excavated to evenly convex; apical ventrite of male with one seta each side, of female with two setae each side. Microsculpture well developed on frons, consisting of isodiametric to slightly transversely stretched sculpticells; pronotum with dense transverse mesh over disc, but with isodiametric mesh medioapically on anterior margin; elytral intervals with dense transverse-line microsculpture; entire body surface with sparse pelage of fine microsetae, microsetae longer on frons and ventral body surface and shorter on pronotal disc and elytra. Coloration of head capsule rufopiceous; antennae pale throughout, brunneotestaceous; pronotum, proepipleuron and prosternum piceous; elytra rufopiceous basally, dark rufous apically; elytral epipleuron rufous; metepisternum piceous; abdomen rufobrunneous, ventrite 6 narrowly rufoflavous apically; femur, tibiae and tarsi flavous.

Male genitalia (n = 1). Male aedeagal median lobe robust, broadly parallel sided from base to apex of ostial



Figures 47–50. Dorsal habitus photographs of *Cyphocoleus* spp.: **47**, *C. lissus* female, Mt. Humboldt; **48**, *C. prolixus* male, Mt. Humboldt; **49**, *C. heterogenus* male, Yahoué; **50**, *C. parovicollis* male, Pic d'Amoa.

opening, dorsoventral breadth at midlength $0.25\times$ distance from tip to base of closed basal bulb (Fig. 51); lobe shaft slightly melanized, the internal sac visible through lobe wall in uneveted position; lobe apex parallel-sided,

length distad ostial opening $2.5\times$ dorsoventral breadth; tip of lobe narrowly rounded, slightly upcurved.

Female reproductive tract ($n = 1$). Bursa copulatrix vase-shaped, basally stalked, distance from base of gono-

coxites to spermathecal basal sclerite $2.75 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 60); bursal walls thin, translucent, with broad band of short spicules lining lumen near midlength; basal gonocoxite with apical fringe of five setae (Fig. 66); apical gonocoxite acuminate with two lateral ensiform setae.

Types. Holotype female (QMB deposited in MNHN): NEW CALEDONIA / Mt. Rembai, 700–900 m / 9 May, 1984 / G. Monteith & D. Cook // QUEENSLAND / MUSEUM LOAN / DATE: April 2004 / No. LE 04.16 (green label) // female habitus photo / J.K. Liebherr 2015 // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / *lissus* / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (5 specimens). NEW CALEDONIA: Aoupinie, top camp, rainforest, 850 m el., Berlese sieved litter, 21°11'S, 165°18'E, 23-xi-2001, Monteith (QMB, 1; lot no. 1045); Ningua Res. camp, 1100 m el., pyrethrum trees & logs, 21°45'S, 166°09'E, 12–13-xi-2001, Burwell & Monteith (QMB, 1; lot no. 8639); Mt. Do, summit, 1000 m el., 21°45'S, 166°00'E, 21–22-xi-2003, Monteith (QMB, 1; lot no. 11421), forest litter 21°45'S, 166°00'E 03-xii-2009, Schuh (NMHW, 1); Mt. Humboldt, moss forest, 1400 m el., night collecting, 21°53'S, 166°24'E, 06-xi-2002, Burwell, Monteith & Wright (QMB, 1; lot no. 11139).

Etymology. The Latinized adjectival species epithet *lissus* is based on the Greek *lissos*, smooth (Brown 1956), signifying the smooth body surface of beetles comprising this species (Fig. 47).

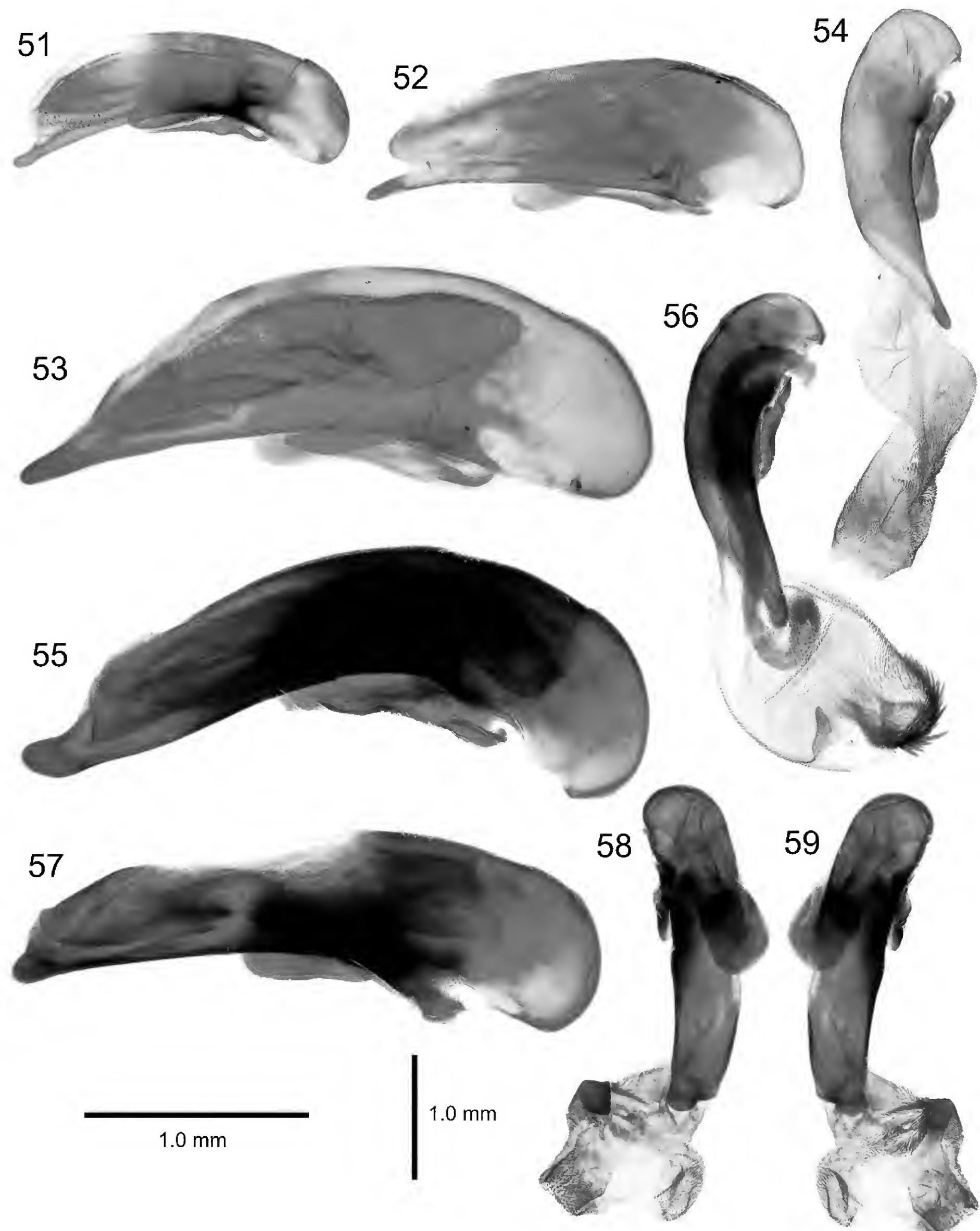
Distribution and habitat. Beetles of this species have been found at elevations from 700–1400 m, at localities ranging from Aoupinie to the north and Mt. Humboldt on the south (Fig. 76). Habitats include moss forest and rainforest, with specimens collected via pyrethrin fog of trees and logs, as well as in ground litter.

2. *Cyphocoleus prolixus* sp. n.

<http://zoobank.org/CE8A36DD-AD17-4CCD-8AF8-76358CCCBBE6>
Figures 48, 52, 61, 67, 77

Diagnosis. These remarkable beetles are uniquely diagnosed by the extremely elongate head and prothorax combined with broad, ovoid elytra (Fig. 48). In keeping with the elongate forebody, the mandibles are exceedingly long, their length $3.2 \times$ distance from anterior margin of antennal articulatory socket to anterolateral margin of labrum, and the antennae are also very elongate: scape length $3.6 \times$ maximum breadth. In stark contrast to *C. lissus* (Fig. 47), the head is broadest just posterad the mandibular articulation, and evenly reduced in width posteriorly to meet the narrow pronotum. The eyes are very small and oriented upward laterad the smooth, broadly convex frons. The elytral setation is also unique within *Cyphocoleus*; only the middle of three dorsal elytral setae present, whereas setae are absent from the anterior and posterior positions. Standardized body length among the largest for *Cyphocoleus* spp.; 11.7–13.1 mm.

Description ($n = 3$). Head capsule broadest anteriorly, a broad flange extended laterally laterad the antennal articulation and before the eye, the posterior articulatory condyle of mandible defining broadest portion of head; neck impression broad and shallow just before juncture of head and prothorax; eyes small though little convex, 17 ommatidia across horizontal diameter of eye; frons broad relative to eyes, ocular ratio 1.23–1.36; supraorbital setae absent; gena setose, a large macroseta present just laterad gula at position slightly posterad hind margin of eye. Pronotum elongate, parallel sided, MPW/PL = 0.44–0.50, broadest near basal third of length; proepimeron bulging outward, visible in dorsal view just laterad and posterad broadest portion of notum; pronotal front angle rounded, not protruded at all; lateral margin of pronotum defined by marginal bead from front angle to just inside subangulate hind angle, median base margined by low, broadly concave ridge; median longitudinal impression very shallow, finely incised; anterior transverse impression shallow, perpendicular to median impression, defining broad, slightly elevated anterior callosity; prosternal process with medially depressed anterior and ventral surfaces, the posterior surface between procoxae convex. Elytra broadly ovoid, the disc relatively flat and sides steeply sloped; discal elytral intervals broadly convex, the associated striae deep, impunctate; parascutellar seta present, articulatory socket not upraised above surface; elytral humeri narrow, humerus distinctly angulate just mesad base of fifth stria; elytral lateral margin distinctly concave laterad anterior series of lateral setae; lateral elytral setae arranged as 6 + 1 + (7)8; subapical and apical elytral setae present; subapical sinuation broadly, shallowly concave, meeting lateral margin at rounded-obtuse angle; elytral apices acutely rounded, slightly separated from each other laterad fused suture. Mesepisternum impunctate; metepisternum subquadrate, dorsal length $1.08 \times$ diagonal width. Legs extremely elongate, femora very thin, mt1 length/tibial length = 0.27; metacoxa bisetose; dorsum of tarsomeres covered with extremely short, sparsely distributed microsetae; mt4 outer lobe $1.56 \times$ median length, 3–4 ventrolateral setae each side. Abdomen with apical margin of apical ventrite broadly and very shallowly excavated to evenly convex; apical ventrite of male with one seta each side, of female with two setae each side. Microsculpture of frons very transverse, densely packed lines only loosely connected into a mesh; pronotal and elytral discs covered with dense transverse lines causing silvery and cupreous iridescence; dorsal body surface bearing a sparse distribution of extremely short microsetae; pro- meso- and metasternum with pelage of longer, more densely distributed setae, abdominal ventrites apparently glabrous except for fixed macrosetae. Coloration of head capsule rufopiceous anterad eyes, piceous toward pronotum; antennae rufobrunneous, palps and maxillae slightly paler, brunneous; pronotum, proepipleuron and proepimeron piceous; elytral disc rufopiceous, elytral epipleura rufopiceous, metepisternum piceous; abdominal ventrites rufobrunneous, apical ventrite 6 narrow rufoflavous apically; femora and tibiae rufobrunneous, tarsi rufoflavous.



Figures 51–59. Male aedeagal median lobe and associated parameres of *Cyphocoleus* spp., dextral view: **51**, *C. lissus*, Mt. Humboldt; **52**, *C. prolixus*, Mt. Humboldt; **53**, *C. heterogenus*, Yahoué; **54**, *C. heterogenus*, internal sac everted, La Foa; **55**, *C. parovicollis*, Me Maoya; **56**, *C. parovicollis*, internal sac everted, Me Maoya; **57**, *C. ovicollis*, Ningua Res.; **58–59**, *C. ovicollis*, internal sac everted, Mt. Do; **58**, laevoventral view; **59**, dextrodorsal view. Scale bars, 1.0 mm: horizontal scale for figures with transverse orientation; vertical scale for figures with vertical orientation.

Male genitalia (n = 1). Male aedeagal median lobe robust, broadest near parameral articulations, slightly narrowed toward distal margin of ostial opening, dorsoventral breadth at midlength $0.3 \times$ distance from tip to base of closed basal bulb (Fig. 52); lobe shaft slightly melanized, the internal sac visible through lobe wall in unverted position; lobe apex parallel-sided, evenly downcurved to narrowly rounded tip, length distad ostial opening $4 \times$ dorsoventral breadth.

Female reproductive tract (n = 1). Bursa copulatrix elongate, columnar, distance from base of gonocoxites to spermathecal basal sclerite $4.5 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 61); bursal walls thin, translucent, densely wrinkled in distal half of bursa; basal gonocoxite with apical fringe of five to six setae (sixth seta smaller) (Fig. 67)

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA 11138 / 21°53'Sx166°24'E. 1400m. / Mt Humboldt, moss forest. / 6–7 Nov 2002. Monteith & / Burwell. pyreth, trees&logs // QUEENSLAND / MUSEUM LOAN / DATE: Nov. 2003 / No. LEN 1688 (green label) // male habitus photo / J.K. Liebherr 2015 // *Cyphocoleus* revision / measured specimen 2 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / *prolixus* / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (2 specimens). NEW CALEDONIA: Mt. Humboldt, moss forest, 1400 m el., pyrethrum trees & logs, 21°53'S, 166°24'E, 06–07-xi- 2002, Monteith & Burwell (QMB, 2; lot 11138).

Etymology. The elongate prothorax exhibited by beetles of this species (Fig. 48) supports use of the adjectival species epithet *prolixus*; i.e. stretched out, long (Brown 1956).

Distribution and habitat. This species is known only from Mt. Humboldt at 1400 m el. (Fig. 77). The three specimens were collected from pyrethrin fog samples of trees and logs within moss forest.

3. *Cyphocoleus heterogenus* Chaudoir, 1877

Figures 28, 49, 53–54, 62, 68, 77

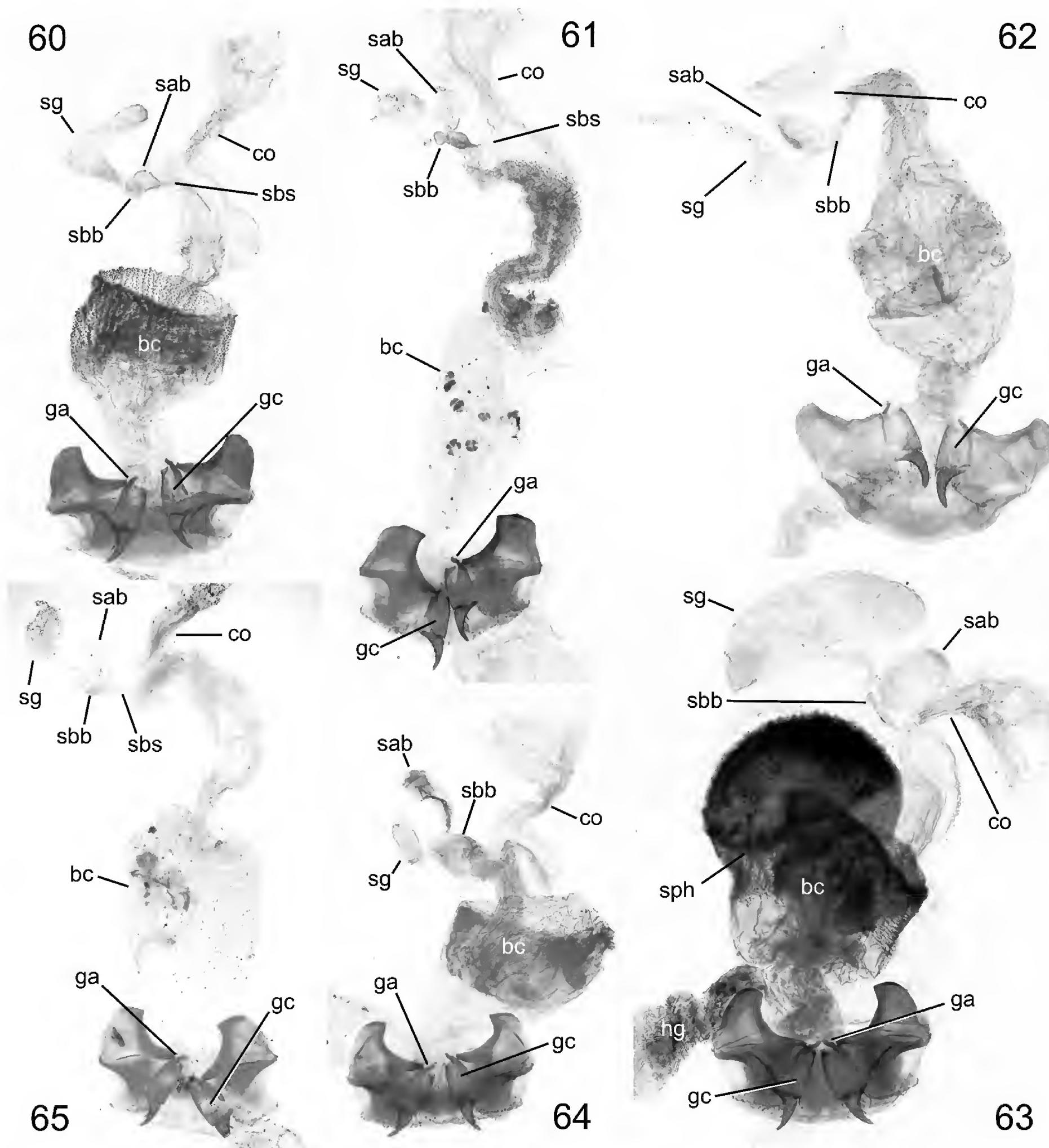
Diagnosis. Beetles as large as *C. prolixus*, standardized body length 10.8–13.1 mm, but head and prothorax much broader, the head much more developed at the expense of pronotal length (Figs 48, 49). Though the mandibles are shorter than in *C. prolixus*, with mandibular length $2.0 \times$ distance from antennal socket to anterolateral margin of labrum, the antennae are longer, with scape length $4.1 \times$ maximal breadth. The pronotum is unique among *Cyphocoleus* due to the extremely elongate, acutely protruded front angles. The presence of three dorsal elytral setae is shared only with *C. ovicollis* (Fig. 82), all other species exhibiting more reduced numbers of dorsal elytral setae or none at all.

Description (n = 5). Head capsule broad, robust, distance from clypeal-labral suture subequal to width across eyes; frons broadly convex, with small chevron-shaped indentation medially between front margins of eyes; eyes

moderately large, convex, 28 ommatidia across horizontal diameter; eyes moderately small, convex, ocular ratio 1.35–1.42; only posterior supraorbital seta present; neck distinctly impressed just before juncture with prothorax; gena glabrous, subgenal seta absent. Pronotum distinctly cordate, margin sinuately constricted basally; lateral marginal bead present from acute front angles to just mesad tightly rounded hind angles; median base margin by fine bead; proepisternum slightly bulging, visible in dorsal view along middle half of prothorax; median longitudinal impression shallow, finely incised; anterior transverse impression broad, shallow, obliquely meeting median impression; anterior callosity slightly convex; prosternal process with fine median ridge anteriorly between procoxae, medially depressed on ventral and posterior face. Elytra broadly ovoid, disc moderately convex with side only moderately depressed relative to disc; elytral striae impunctate; parascutellar seta present, articulatory socket not upraised above elytral surface; elytra narrow basally, humeri obtuse-angulate at base of fifth stria; lateral margin straight to slightly concave lateral anterior series of lateral elytral setae; lateral elytral setae arranged as 6 + 1 + 7–8; subapical and apical elytral setae present; subapical sinuation distinctly invaginated, curvature greatest just mesad obtusely rounded juncture of sinuation and lateral margin. Mesepisternum impunctate; metepisternal dorsal length $0.86 \times$ diagonal width. Abdomen of males with apical margin of apical ventrite distinctly notched, the invagination smoothly rounded; apical ventrite of male with one seta each side, of female with two setae each side. Legs elongate, gracile, mt1 length/tibial length = 0.26; metacoxae bisetose; tarsomeres with short sparse setae dorsally; mt4 outer lobe $1.7 \times$ median length, 4–5 ventrolateral setae each side. Microsculpture of frons and vertex a stretched isodiametric mesh; pronotal disc and discal elytral intervals covered with fine transverse lines; dorsal surface of body apparently glabrous except for standard macrosetae; pro-, meso-, and metasternum and visible abdominal ventrites with sparsely distributed pelage of very short setae. Coloration of dorsum rufopiceous with cyanotic to cupreous iridescence due to microsculpture; antennae dark rufous, paler apically, palps brunneous; basal abdominal ventrites rufopiceous, ventrite 6 rufobrunneous, margin narrowly brunneous; femora rufopiceous, tibiae rufobrunneous, tarsi slightly paler, dark rufous.

Male genitalia (n = 8). Male aedeagal median lobe robust, broadly parallel sided in basal 3/4 of length, then evenly narrowed to projected, narrow tip, dorsoventral breadth at midlength $0.25 \times$ distance from tip to base of closed basal bulb (Fig. 53); lobe shaft slightly melanized, the internal sac visible through lobe wall in unverted position; lobe apex tapered to tightly rounded tip, length distad ostial opening $2.5 \times$ dorsoventral breadth; internal sac evenly covered with short melanized spicules in distal half, of sinuous shape but sides parallel in extension (Fig. 54).

Female reproductive tract (n = 2). Bursa copulatrix vase-shaped, basally stalked, distance from base of gono-



Figures 60–65. Female reproductive tract, ventral view, for *Cyphocoleus* spp.; **60**, *C. lissus*, Mt. Humboldt; **61**, *C. prolixus*, Mt. Humboldt; **62**, *C. heterogenus*, Yahoué; **63**, *C. parovicollis*, Mandjélia; **64**, *C. monteithi*, Mt. Mou; **65**, *C. miricollis*, Forêt Nord. For abbreviations see Table 1.

coxites to spermathecal basal sclerite $2.4\times$ maximum breadth (dissection compressed under cover slip) (Fig. 62); bursal walls thin, translucent, with broad band of spicules lining lumen near midlength; basal gonocoxite with apical fringe of seven to eight setae (Fig. 68); apical gonocoxite broadly rounded at apex with three lateral ensiform setae.

Type. Holotype male (MNHN): Ex Musæo / Chaudoir (red-inked white label with red border) // HOLOTYPE / *Cyphocoleus* / *heterogenus* / Chaudoir 1877 (black-bor-

dered red label). Holotype status is based on Chaudoir's (1887: 193) statement "Cet insecte m'a été cédé par M. Sallé." Yahoué hereby designated type locality.

Distribution and habitat. Found throughout Grande Terre, from Mt. Ignambi and Mt. Panié on the north, to Forêt de Thi on the south (Fig. 77, Suppl. material 3). Beetles have been collected from pyrethrin spray samples from trees and logs, with and without epiphytes, from under a rock near a dead tree, from *Freycinetia* axils, and by hand during night.

4. *Cyphocoleus parovicollis* sp. n.

<http://zoobank.org/8894D2DB-88B0-4205-B69F-9C4A8C34245D>

Figures 50, 55–56, 63, 69, 78

Diagnosis. This species and its following adelphotaxon are difficult to diagnose practically (Figs 50, 82), yet are clearly separate species. They can be diagnosed by the more convex eyes in beetles of this species, ocular ratio 1.47–1.55, and presence of four apical abdominal setae in males – two setae each side of apical visible abdominal ventrite – versus two apical abdominal setae – one each side – in males of *C. ovicollis*. The pronotum is generally narrower basally among individuals of this species – MPW/BPW = 1.87–2.10 – but the values overlap in the two species, with individuals of *C. ovicollis* ranging in values 2.04–2.29 for the same ratio. If a male is available, the identity based on abdominal setation can be confirmed based on the very different aedeagal internal sacs: that of *C. parovicollis* exhibiting an apical “cockscomb” of large, densely pack macrotrichia (Fig. 56). The allopatric geographic distributions can assist in the sorting of these two species, with *C. parovicollis* distributed to the north of *C. ovicollis* (Fig. 78). Standardized body length 9.4–12.1 mm.

Description (n = 5). Head capsule moderately broad, gena elongate anterad constricted neck (Fig. 50); frons broadly convex, but with variably developed chevron-shaped depression medially between eyes; supraorbital setae absent; mandibles elongate, length 2.5× distance from antennal articulatory socket to anterolateral margin of labrum; antennae very elongate, scape length 4.33× maximal breadth; supraorbital setae absent; gena glabrous, subgenal seta absent. Pronotum narrowly obovoid, MPW/PL = 0.78–0.88; front angles slightly protruded, right to slightly obtuse; lateral marginal bead continuous to obtuse-rounded basal angles and across straight median base; proepisternum bulging outward and so visible in dorsal view for middle half of pronotal length; median longitudinal impression deep, finely incised, terminated posteriorly in variably developed transverse depression; anterior transverse impression very shallow, obliquely paralleling anterior pronotal margin; prosternal process indistinctly depressed medially on ventral surface. Elytra narrowly subellipsoid, MEW/EL = 0.65–0.70; disc broadly and moderately convex; elytral striae deep, impunctate, associated intervals broadly convex; parascutellar seta present, socket not upraised above elytral surface; humeri very narrow, distinctly obtuse-angulate at base of fifth stria; elytral lateral margin convex laterad anterior series of lateral elytral setae; two to three dorsal elytral setae present (setae at anterior and middle positions always present, posterior seta present or absent); lateral elytral setae arranged as 6+ 1(0) + 7; subapical and apical setae present; subapical sinuation broadly and slightly concave, joining lateral margin in a broad curve; elytral apices tightly rounded, slightly separated from suture. Mesepisternum impunctate; metepisternum dorsal length 0.93× diagonal width. Abdomen of males with distinct, narrow notch medially on apical margin of apical ventrite; females with two setae each side on apical margin of api-

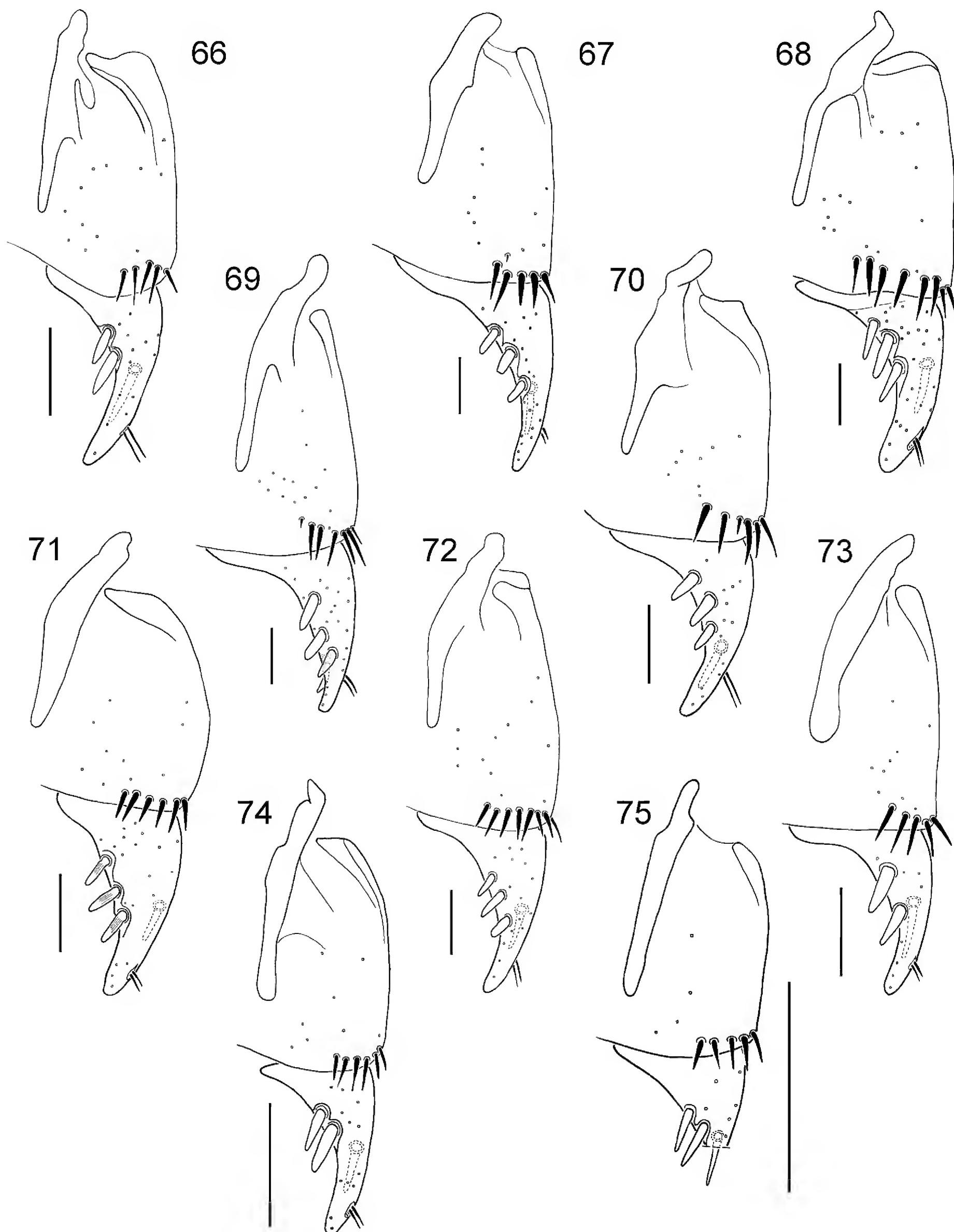
cal ventrite. Legs elongate, gracile, mt1 length/tibial length 0.26; metacoxae bisetose; tarsomeres with short, sparse seta on dorsum; mt4 outer lobe 1.5× median length, 4–5 lateroventral setae each side. Microsculpture of frons transversely stretched isodiametric mesh to distinctly transverse mesh on vertex; pronotal disc with dense transverse-line microsculpture loosely organized into a mesh; elytral disc with dense transverse lines resulting in cyanotic to cupreous iridescence; pro-, meso-, and metasternum with sparse pelage of short microsetae, abdominal ventrites and dorsal body surface apparently glabrous. Coloration of head capsule rufopiceous, antennae rufobrunneous with piceous cast on antennomeres 1–3; pronotum piceous, proepipleuron and proepisternum rufopiceous; elytra rufopiceous; elytral epipleuron rufous, metepisternum rufopiceous; femora and tibiae rufobrunneous, tarsi rufoflavous.

Male genitalia (n = 4). Male aedeagal median lobe robust, broadly parallel sided to near distal margin of ostial opening, dorsoventral breadth at midlength 0.2× distance from tip to base of closed basal bulb (Fig. 55); lobe shaft brunneous, the internal sac obscured in uneveted position by the moderately melanized lobe wall; lobe apex with broadly rounded tip, tip skewed toward the left side of lobe, length distad ostial opening only slightly more than breadth; internal sac with apical “cockscomb” composed of densely packed, elongate, melanized, spike-like macrotrichia, the sac broadest at midlength (Fig. 56).

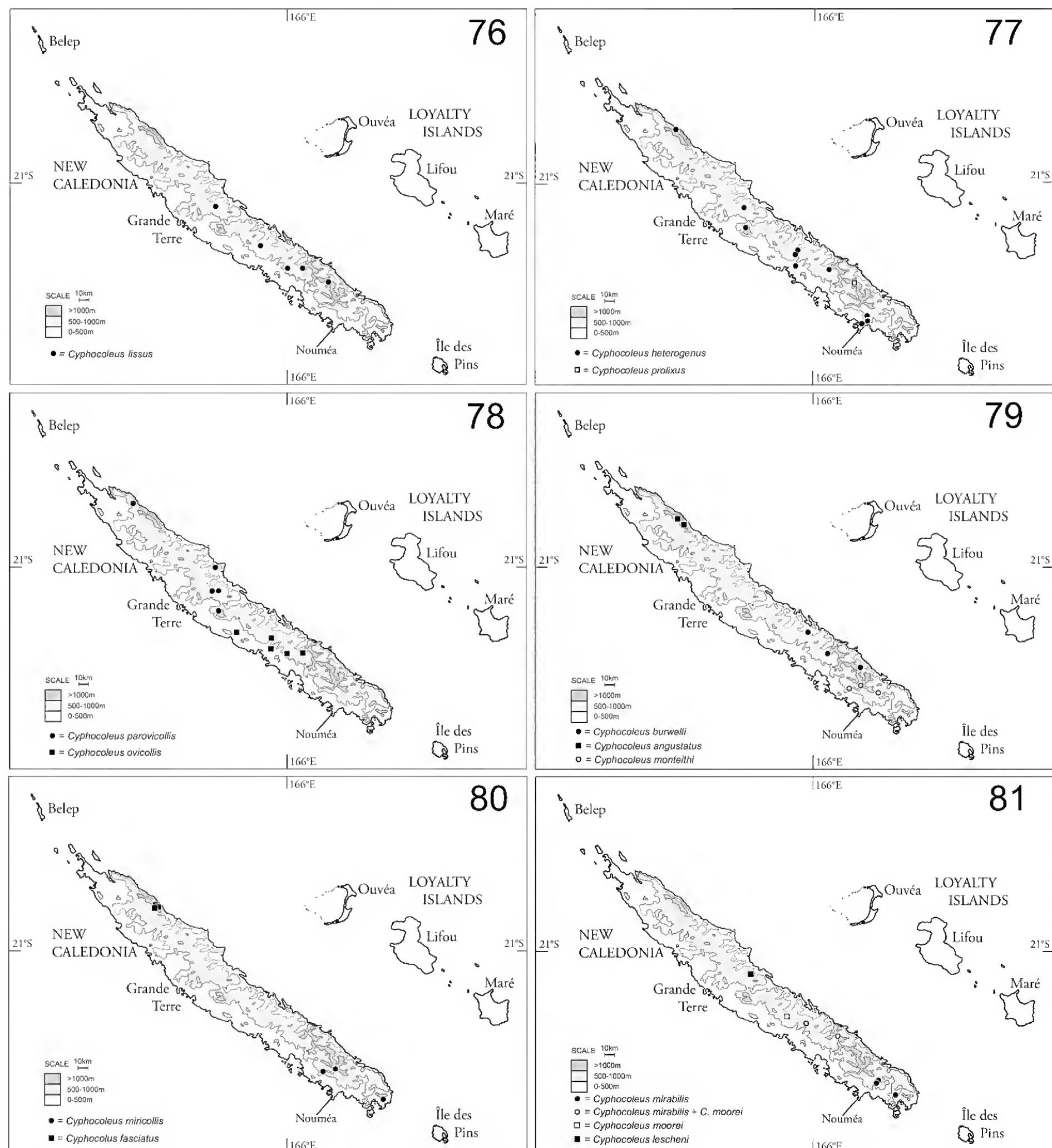
Female reproductive tract (n = 2). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite 1.8× maximum breadth (dissection compressed under cover slip) (Fig. 63); bursal walls thick, heavily pigmented by Chlorazol Black stain, with broad band of thick, densely packed spicules lining lumen over broadest part of bursa; basal gonocoxite with apical fringe of six setae, an additional small seventh seta observed in one individual (Fig. 69); apical gonocoxite acuminate with narrowly rounded apex and three lateral ensiform setae.

Type. Holotype male (QMB deposited in MNHN): NEW CALEDONIA 8682 / 20°58'Sx165°17'E.500m / Pic d'Amoa, N slopes / 24Nov2001. GBMonteith / Pyrethrum, trees & logs // QUEENSLAND / MUSEUM LOAN / Date: Nov. 2003 / no. LEN-1688 (green label) // Cyphocoleus / n. sp. / ovicollis male 9 / det. J.K. Liebherr 2015 // genitalia vial // HOLOTYPE / Cyphocoleus / parovipennis / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (30 specimens). NEW CALEDONIA: Mandjélia, above Pouébo 600–750 m el., 20°24'S, 164°32'E, 11–13-v-1984, Monteith & Cook (QMB, 1); Mt. Panié refuge, 1300 m el., 20°34'S, 164°46'E, 16–18-xi-2000, Bouchard, Burwell & Monteith (QMB, 1; lot no. 9938); Pic d'Amoa, N slopes, 500 m el., hand collecting, 20°58'S, 165°17'E, 10–11-xi- 2001, Burwell & Monteith (QMB, 1; lot no. 8687); Aoupinié, 850 m el., 21°11'S, 165°19'E, 20–21-xi-2000, Bouchard, Burwell & Monteith (QMB, 2; lot no. 9930), summit, 1000 m el., pyrethrum trees & logs, 21°11'S, 165°16'E, 02-x-2004, Monteith (QMB, 1; lot no. 11665), 21°11'S, 165°19'E,



Figures 66–75. Female right gonocoxae, ventral view, for *Cyphocoleus* spp. illustrating apical fringe setae of basal gonocoxite 1, and two or three lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae on apical gonocoxite 2; **66**, *C. lissus*, Mt. Humboldt; **67**, *C. prolixus*, Mt. Humboldt; **68**, *C. heterogenus*, Yahoué; **69**, *C. parovicollis*, Mandjélia; **70**, *C. ovicollis*, Ningua Res.; **71**, *C. burwelli*, Mt. Humboldt; **72**, *C. monteithi*, Mt. Mou; **73**, *C. miricollis*, Forêt Nord; **74**, *C. mirabilis*, Mt. Koghi; **75**, *C. lescheni*, apical gonocoxite damaged, Aoupinié. Scale bar, 0.10 mm.



Figures 76–81. Distribution maps of *Cyphocoleus* spp.: 76, *C. lissus*; 77, *C. heterogenus*, *C. prolixus*; 78, *C. parovicollis*, *C. ovicollis*; 79, *C. burwelli*, *C. angustatus*, *C. monteithi*; 80, *C. miricollis*, *C. fasciatus*; 81, *C. mirabilis*, *C. moorei*, *C. lescheni*.

12-xii-1993, Raven (QMB, 1); Me Maoya, near summit, 1400 m el., pyrethrum trees & logs, 21°22'S, 165°20'E, 12-xi-2002, Burwell & Monteith (QMB, 1; lot no. 11163); Me Maoya camp, 1150 m el., night collecting, 21°22'S, 165°20'E, 11–12-xi- 2002, Burwell, Monteith & Wright (QMB, 15; lot no. 11159), pyrethrum trees & logs, 11–13-xi-2002, Monteith & Burwell (QMB, 5; lot no. 11158); Me Maoya, near summit, 1300 m el., pyrethrum trees & logs, 21°22'S, 165°20'E, 12-xi-2002, Monteith & Burwell (QMB, 2; lot no. 11169).

Etymology. The adelphotaxon status and great similarity of this species and *C. ovicollis* (Figs 46, 50, 82) is signified through use of parovicollis as this species' epithet: i.e. equal to ovicollis.

Distribution and habitat. This species is distributed in the northern half of Grande Terre, allopatric with its adelphotaxon, *C. ovicollis*, which is distributed to the south (Fig. 78). Beetles have been collected from tree trunks and downed logs via pyrethrin fog, and also by hand collecting at night.

5. *Cyphocoleus ovicollis* Fauvel, 1882

Figures 57–59, 70, 78, 82

Diagnosis. In juxtaposition to its cryptic adelphotaxon, this species can be diagnosed by the flatter eyes, ocular ratio 1.41–1.44, and presence of two apical abdominal setae in the males of this species – one seta each side of apical visible abdominal ventrite – versus four apical abdominal setae – two each side – in males of *C. parovicollis*. The pronotum is generally broader basally among individuals of this species – MPW/BPW = 2.04–2.29 – versus values of 1.87–2.10 in *C. ovicollis*. A male dissection will allow attribution of a series of specimens, with the male of *C. ovicollis* exhibiting an internal sac with a robust, mound-shaped tooth on the right side (Figs 58, 59). The allopatric geographic distributions also provide information as *C. ovicollis* (Fig. 78) is distributed to the south of *C. parovicollis*. Standardized body length 9.1–11.0 mm.

Description (n = 5). (The description of *C. parovicollis* can serve for this species, with the following exceptions). Head capsule with mandibles elongate, length 2.4× distance from antennal articulatory socket to anterolateral margin of labrum. Elytra more broadly subellipsoid, MEW/EL = 0.71–0.73; three dorsal elytral setae uniformly present; lateral elytral setae arranged as 6 + 1(0) + 7(8). Mesepisternum dorsal length 0.8× diagonal width.

Male genitalia (n = 5). Male aedeagal median lobe robust, broadly parallel sided in basal half, then tapered to narrowly rounded tip, dorsoventral breadth at midlength 0.2× distance from tip to base of closed basal bulb (Fig. 57); lobe shaft brunneous, the internal sac obscured in un-everted position by the moderately melanized lobe wall; lobe apex with evenly rounded tip, length distad ostial opening subequal to breadth; internal sac broadest at mid-length, with large sclerotized plaque-like tooth on right side, and a ring of melanized microtrichia apically near gonopore (Figs 58, 59).

Female reproductive tract (n = 1). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite 1.7× maximum breadth (dissection compressed under cover slip) (as in Fig. 63); bursal walls thick, heavily pigmented by Chlorazol Black stain, with broad band of thick, densely packed spicules lining lumen over broadest part of bursa; basal gonocoxite with apical fringe of six to seven setae (Fig. 70); apical gonocoxite acuminate with narrowly rounded apex and three lateral ensiform setae.

Type. Holotype male (MNHN): C. ovicollis / Fvl. // Ex-Musæo / Mniszech (white label with black border) // HOLOTYPE / Cyphocoleus / ovicollis / Fauvel 1882 (black-bordered red label). Type locality noted by Fauvel (1882: 248) as “probablement à Ourail,” with Bourail hereby designated type locality.

Distribution and habitat. The known distribution northern portions of Province Sud, from Bourail and Col d'Amieu on the north to Mt. Do and Ningua Reserve to the south (Fig. 78, Suppl. material 3). Specimens have been obtained in pyrethrin samples from trunks and logs

with and without epiphytes, via hand collecting, with one series of six specimens collected in a flight intercept trap, without doubt having climbed onto and into the trap.

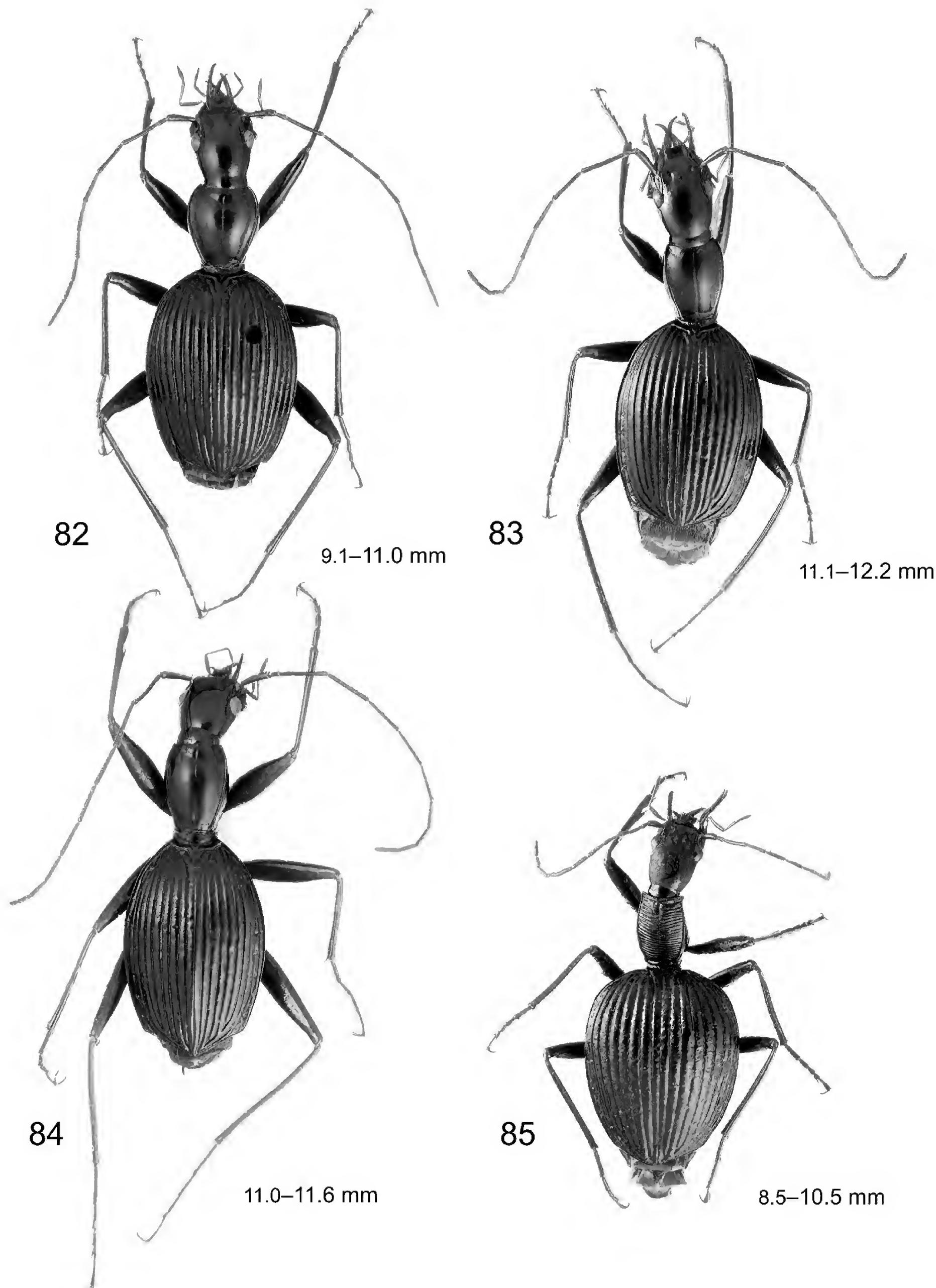
6. *Cyphocoleus burwelli* sp. n.

<http://zoobank.org/B5B3D4B3-E303-4330-B69C-7EB910795E93>

Figures 71, 79, 83, 86

Diagnosis. This species and the following, *C. angustatus*, comprise a second sibling species pair, these two characterized by the narrow body: i.e. pronotum and elytra. The pronotum of *C. burwelli* is more evenly ovate, with MPW/BPW = 1.72–1.83 versus values of 1.84–1.91 for *C. angustatus*. The pronotum is also relatively narrower overall, with MPW/PL = 0.68–0.72 compared to values of 0.72–0.77 recorded for *C. angustatus*. The elytra are narrower basally in *C. burwelli*, with MEW/HuW = 2.78–3.19 versus 2.60–2.79 for *C. angustatus*, and the humeral angle is obtuse versus very distinctly right angled to slightly acute in *C. angustatus* (Figs 83, 84). A male dissection can be used to confirm this diagnosis, with the aedeagal median lobe apex narrowly rounded in this species, and the internal sac bearing a stout apical tooth (Fig. 86). Standardized body length 11.1–12.2 mm.

Description (n = 4). Head capsule moderately elongate, trapezoidal, with broad flange basad posterior mandibular articulation, neck distinctly constricted (Fig. 83); frons broadly convex between hind margin of eyes, with shallow median dimple and progressively broadened frontal grooves anteriorly; eyes small and little convex, 23–28 ommatidia across horizontal diameter; supraorbital setae absent; mandibles elongate, length 2.4× distance from antennal articulatory socket to lateroapical margin of labrum; antennae elongate, scape length 4.2× maximal breadth; subgenal seta absent. Pronotum with front angles only slightly protruded, obtuse angulate; lateral marginal bead continuous to just mesad evenly rounded hind angles, basal margin not beaded medially; proepipleuron and proepisternum bulging outward in basal half of pronotal length, visible in dorsal view; median longitudinal impression shallowly and finely incised, wavering along length; anterior transverse impression very shallow, barely traceable as oblique impression that reaches lateral marginal bead behind front angle; prosternal process flat anteriorly, flat to slightly depressed medially on ventral surface, convex posteriorly between procoxae. Elytra narrowly ellipsoid, moderately convex; elytral striae deep, impunctate, associated intervals moderately convex; parascutellar seta present, articulatory socket not upraised above surface of elytra; humeral angles obtuse-angulate, the juncture of basal and marginal grooves tightly rounded; lateral margin evenly convex outside anterior series of lateral elytral setae; two to three dorsal elytral setae present (setae at anterior and middle position present or absent, seta at posterior position always present); lateral elytral setae arranged as 6 + (7)8; subapical and apical elytral setae present; subapical sinuation slightly, evenly concave, sinuation meet-



Figures 82–85. Dorsal habitus photographs of *Cyphocoleus* spp.: **82**, *C. ovicollis* female, Ningua Res.; **83**, *C. burwelli* female, Mt. Canala; **84**, *C. angustatus* male, Mt. Panié; **85**, *C. monteithi* male, Dzumac Rd. jct.

ing lateral margin in broadly convex curve; elytral apices rounded, the apical margin invaginated to meet fused elytral suture. Mesepisternum impunctate; metepisternal dorsal length $0.9 \times$ diagonal width. Abdomen of males with apical ventrite distinctly notched medially; two setae on apical margin of apical ventrite in males (one seta each side), four setae (two each side) present on apical margin of females. Legs elongate, gracile, mt1 length/tibial length = 0.27; metacoxae bisetose; tarsomeres with short, sparsely distributed setae on dorsal surface; mt4 length of outer lobe $1.3 \times$ median length, 6–8 ventrolateral setae each side. Microsculpture of frons isodiametric, longitudinally stretched near median dimple, head microsculpture transversely stretched on clypeus and further posterad on vertex, becoming dense transverse lines before neck constriction; pronotal and elytral disc with dense transverse-line microsculpture; pro-, meso-, and metasternum, metacoxae and abdominal ventrites with sparsely distributed pelage of moderately elongate microsetae. Coloration of head and pronotum piceous with metallic cyanotic iridescence due to microsculpture; elytra rufopiceous with similar iridescence; ventral body surface uniformly dark, piceous to rufopiceous on medial portions of apical three abdominal ventrites, apical ventrite with pale, rufoflavous apical margin; legs slightly paler than ventrites, femora and tibiae rufobrunneous with piceous cast, tarsi brunneous.

Male genitalia (n = 1). Male aedeagal median lobe robust, broadly parallel sided in basal half, then tapered to rounded tip, dorsoventral breadth at midlength $0.3 \times$ distance from tip to base of closed basal bulb (Fig. 86); lobe shaft brunneous, the internal sac obscured in unevolved position by the moderately melanized lobe wall; lobe apex with tapered tip, length distad ostial opening subequal to breadth; internal sac broadest at midlength, with extremely large sclerotized apical tooth and a broad ring of melanized macrotrichia over middle half of sac (Fig. 86).

Female reproductive tract (n = 1). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite $1.4 \times$ maximum breadth (dissection compressed under cover slip) (as in Fig. 63); bursal walls thick, heavily pigmented by Chlorazol Black stain, with broad band of thick, densely packed spicules lining lumen over broadest part of bursa; basal gonocoxite with apical fringe of six to seven setae (Fig. 71); apical gonocoxite triangular with rounded apex (due to wear?) and three lateral ensiform setae.

Types. Holotype female (MNHB deposited in MNHN): Drs. F. Sarasin & J. Roux / Neukaledonien / Mt. Humboldt (on obverse of blue label) / Gipsel, 1600 m. / 18.9.1911 (on reverse of blue label) // *Cyphocoleus* / ovicollis Fauv. / Det. K.M. Heller 1914 // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / burwelli / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (3 specimens). NEW CALEDONIA: Ningua Reserve, near summit, 1300 m el., $21^{\circ}45'S$, $166^{\circ}09'E$, 13-xi-2001, Burwell & Monteith (QMB, 1); Mt. Humboldt, 1600 m el., $21^{\circ}53'S$, $166^{\circ}26'E$, 18-ix-1911, Sarasin

& Roux (SMTD, 1); Mt. Kanala, Wald, 800–1000 m el., $21^{\circ}34'S$, $165^{\circ}56'E$, 04-xi-1911, Sarasin/Roux (MNHB, 1).

Etymology. This species is named for Dr. Chris Burwell, Senior Curator of Insects, Queensland Museum, in recognition of the numerous specimens of *Cyphocoleus* he has collected: many representing previously undescribed species.

Distribution and habitat. The distribution of this species ranges from Mt. Humboldt on the south, to Mt. Canala on the north (Fig. 79). Collection sites range in elevation from 1000–1600 m.

7. *Cyphocoleus angustatus* sp. n.

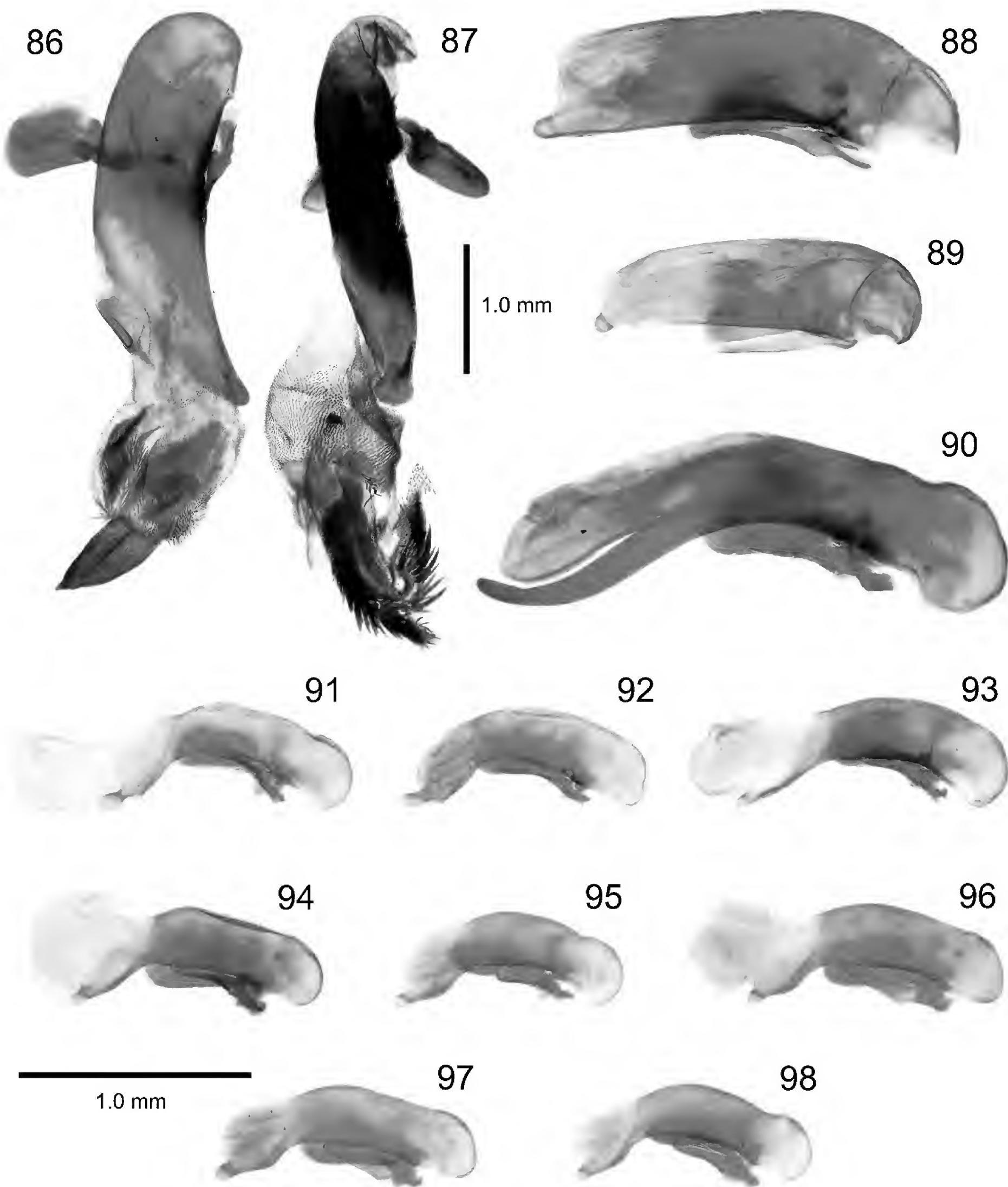
<http://zoobank.org/E414FE48-C4B8-4AF4-A7CA-3D377AE806EA>

Figures 29, 79, 84, 87

Diagnosis. As the second half of the sibling species pair also including *C. burwelli*, this species can be diagnosed by the more basally constricted pronotum, MPW/BPW = 1.84–1.91 versus values of 1.72–1.83 for *C. burwelli*. The pronotum is also relatively broader overall, with MPW/PL = 0.72–0.77 versus values of 0.68–0.72 for *C. burwelli*. The elytra are broader basally in *C. angustatus*, with MEW/HuW = 2.60–2.79 versus 2.78–3.19 for *C. burwelli*. The humeral angle is positioned more anteriorly relative to the scutellum, and is very distinctly right angled to slightly acute in this species (Fig. 84). If a male can be dissected, the aedeagal median lobe apex is broadly expanded in this species, and the internal sac bears an apical “cockscomb” of densely packed macrotrichia (Fig. 87). Standardized body length 11.0–11.6 mm.

Description (n = 3). (The description of *C. burwelli* can serve for this species, with the following exceptions). Head capsule with mandibles exceedingly elongate; length $4.9 \times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae exceedingly elongate, gracile, scape length $4.9 \times$ maximal breadth. Pronotum margined basally with narrow, little upraised bead crossing median base between the distinctly margined, rounded hind angles. Elytra narrowly ovoid, extremely narrow basally; two dorsal elytral setae present at positions of middle and posterior seta; lateral elytral setae arranged as 6 + 1 + 7, or 6 + 8. Legs extremely elongate, gracile; metacoxae trisetose, two setae on lateral surface fore and aft, and a third large seta medial to posterior seta (short setae comprising part of ventral pelage also present); mt4 with length to apex of outer lobe $1.45 \times$ median tarsomere length. Coloration of legs paler than piceous thoracic and rufopiceous abdominal ventrites, femora dark rufous with piceous cast, tibiae rufobrunneous, and tarsi paler, brunneous to rufoflavous.

Male genitalia (n = 2). Male aedeagal median lobe robust, broadly parallel sided to near distal margin of ostial opening, dorsoventral breadth at midlength $0.2 \times$ distance from tip to base of closed basal bulb (Fig. 87); lobe shaft melanized, the internal sac obscured in unevolved position by the moderately melanized lobe wall; lobe apex with



Figures 86–98. Male aedeagal median lobe and associated parameres of *Cyphocoleus* spp., dextral view: 86, *C. burwelli*, internal sac everted, Ningua Res.; 87, *C. angustatus*, dextroventral view, internal sac everted, Mt. Panié; 88, *C. monteithi*, Parque Prov. Rivière Bleue, Haute Pourina; 89, *C. miricollis*, Mt. Mou; 90, *C. fasciatus*, dextral view, sac partially everted, Mt. Panié; 91–98, *C. cychroides*; 91, internal sac everted, Mandjélia; 92–93, Mandjélia; 94, internal sac everted, Hienghène; 95, Touho; 96, Tionaka Tal; 97, Ateou; 98, Pic d’Amoa. Scale bars, 1.0 mm: horizontal scale for figures with transverse orientation; vertical scale for figures with vertical orientation.

very broadly rounded tip, length distad ostial opening less than breadth; internal sac with well-developed apical “cockscomb” composed of densely packed, elongate,

melanized, spike-like macrotrichia, the basal half of sac densely covered with short, melanized microtrichia.

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA / Mt Panié, 1300 m / 3-xi-1988 / R. Raven // QUEENSLAND / MUSEUM LOAN / DATE: Jan. 2004 / No. LE 04.01 (green label) // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 male 2 // HOLOTYPE / *Cyphocoleus angustatus* / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (7 specimens). NEW CALEDONIA: Mt. Panié, 730 m el., under stones amongst ants, 20°32'S, 164°44'E, 24-viii-1914, Montague (BMNH, 2), 28-viii-1914, Montague (BMNH, 1), 1300 m el., 20°34'S, 164°46'E, 03-xi-1988, Raven (QMB, 1), refuge, 1350 m el., 20°34'S, 164°46'E, 08–09-xi-2001, Balke & Wewalka (ZSM, 2).

Etymology. The narrow, elongate pronotum and very narrow elytral humeri (Fig. 84) suggest the adjectival species epithet, *angustatus*, based on the Latin *angustus*, or narrow (Brown 1956).

Distribution and habitat. This species is known only from Mt. Panié, with localities at 730 m elevation in 1914, and from 1300–1350 m elevation for more recently collected material (Fig. 79). P. D. Montague's specimens (see Turner 1919) are labeled as being collected “under stones amongst ants”, although the level of interaction among beetles and ants, if any, is not known.

8. *Cyphocoleus monteithi* sp. n.

<http://zoobank.org/B88459B2-D6F8-486A-B85A-37EA2EA0135A>

Figures 64, 72, 79, 85, 88

Diagnosis. This species (Fig. 85) shares the very elongate prothorax and narrow head with *C. prolixus* (Fig. 48), however the pronotal disc is transversely wrinkled and the pronotal front angles are acutely extended as in *C. miricollis* below. These characters support this species' phylogenetic intercalation subordinate to the former, and as adelphotaxon to the latter plus all cladistically associated species (Fig. 45). The elytra are distinctly ovate and very convex, domed, the lateral intervals and margins very depressed relative to the disc. This is also the first of the species to be treated in this revision that bears an environmental patina: in this species a varnish-like coating that covers the body surface of the beetles, this coating deepest in depressed areas such as the transverse pronotal wrinkles and elytral striae. Body surfaces on the mouthparts, antennae, and at the base of the head between the constricted neck and anterior prothoracic margin are dramatically clear of this varnish. Standardized body length 8.5–10.5 mm.

Description (n = 5). Head capsule ellipsoid, genal surfaces behind eyes subparallel, then converging to distinctly constricted neck; frons with broad medial crest between eyes, fine arcuate wrinkles curving outward and posterad from crest, frontal grooves parallel, broadly depressed from position between hind margins of eyes to clypeus, broadest just posterad frontoclypeal suture; eyes small, convex, 20 ommatidia across horizontal diameter,

ocular ratio 1.39–1.50; supraorbital setae absent; mandibles moderately elongate, length 2.4× distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length 2.6× maximal breadth; gena setose, subgenal seta present just laterad gula about 2/3 distance from hind margin of eye to constricted neck. Pronotum elongate, tubular, MPW/PL = 0.59–0.69, base constricted relative to apex, APW/BPW = 1.28–1.40; median longitudinal impression finely and shallowly incised, causing interruptions in orientation of transverse wrinkles in some instances; anterior transverse impression broad, shallow, extended laterally to behind front angles; proepisternum bulging, extended beyond marginal bead of notum, with distinct, deeply engraved vertical wrinkles; prosternal process distinctly depressed medially anterad procoxae, flat to narrowly depressed medially on ventral surface, narrowly convex on posterior surface. Elytra inflated, based inflexed at scutellum and depressed along suture, intervals 3–5 convexly elevated; striae smooth with very widely spaced micropunctures along length (view cleaned specimen); parascutellar seta present, articulatory socket papillate, elevated above surrounding elytral surface; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, their articulatory sockets slightly upraised above surrounding cuticle, often appearing clear of cuticular varnish; subapical and apical elytral setae present, articulatory sockets papillate and clear of varnish; subapical sinuation moderately concave, meeting lateral margin in broad curve; elytral apices rounded, moderately separated by invaginated margin at fused suture. Mesepisternum impunctate, metepisternal dorsal length 1.1× diagonal width. Abdomen with apical ventrite broadly, slightly concave medially; males with one seta each side apical margin of apical ventrite, females with two setae each side. Legs gracile, moderately elongate, mt1 length/tibial length = 0.27; metacoxae bisetose; tarsomeres with dorsal surface glabrous; mt4 with length to apex of outer lobe 1.8× median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture of head transverse, dense; pronotal and elytral disc with fine transverse lines; pro-, meso-, and metasternum plus abdominal ventrites with sparse pelage of extremely short microsetae, such extremely short setae also visible on head on frons, pronotum, and elytra (though cleaning the surface may remove setae). Coloration of head piceous, mandibles rufobrunneous, palps and antennae rufoflavous; pronotum, elytra and body ventrites and coxae piceous; femora piceous with rufobrunneous base and apex, tibiae rufopiceous dorsally, rufobrunneous on lateral and ventral surfaces, tibiae rufobrunneous.

Male genitalia (n = 6). Male aedeagal median lobe robust, broadly parallel sided from base to apex of ostial opening, dorsoventral breadth at midlength 0.25× distance from tip to base of closed basal bulb (Fig. 88); lobe shaft slightly melanized, the internal sac visible through lobe wall in unverted position; lobe apex parallel-sided, length distad ostial opening subequal to dorsoventral breadth; tip of lobe evenly, narrowly rounded.

Female reproductive tract ($n = 1$). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite $1.8 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 64); bursal walls thin, translucent basally, thicker and more heavily stained with Chlorazol Black stain near midlength, lumen without spicules, but bursal surface wrinkled in distal half; basal gonocoxite with apical fringe of seven to eight setae (Fig. 72); apical gonocoxite acuminate with narrowly rounded apex and three lateral ensiform setae.

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA 11152 / 22°02'Sx166°28'E. 950m. / Dzumac Rd., junction / 26Jan2004. G.Monteith / pyrethrum, trees & logs // QUEENSLAND / MUSEUM LOAN / DATE: April 2004 / No. LE 04.16 (green label) // male habitus photo 1 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / monteithi / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (22 specimens). NEW CALEDONIA: Mt. Ouin, 1100 m el., pyrethrum trees & logs, 22°01'S, 166°28'E, 09-xi-2002, Burwell & Monteith (QMB, 1; lot no. 11150); Dzumac Road junction, 950 m el., 22°02'S, 166°28'E, 09-xi-2002, Burwell, Monteith & Wright (QMB, 1; lot no. 11145), pyrethrum trees & logs, 09-xi-2002 Burwell & Monteith (QMB, 3; lot no. 11143), pyrethrum mossy trees, 04-xii-2003, Monteith (QMB, 3; lot no. 11458), pyrethrum trees & logs, 26-i-2004, Monteith (QMB, 8; lot no. 11522), flight intercept trap, 05-xii-2003–26-i-2004, Monteith (QMB, 1; lot no. 11465); Mt. Dzumac road, 700 m el., pyrethrum trunks & logs, 22°03'S, 166°28'E, 01-xii-2000, Monteith (QMB, 1; lot no. 9913); Mt. Mou summit, 1200 m el., 22°04'S, 166°21'E, 24-v-1984, Monteith & Cook (ANIC, 1; QMB, 1), moss forest, 1200 m el., hand collecting, 27–28-xii-2004, Monteith (QMB, 1; lot no. 12019); Rivière Bleue, Haute Pourina, 800 m el., pyrethrum trees & logs, 22°06'S, 166°38'E, 22-xi-2002, Monteith (QMB, 1; lot no. 11210).

Etymology. I take great pleasure in naming this extremely distinctive species (Fig. 85) for Dr. Geoff Monteith, Senior Curator of Insects Emeritus, Queensland Museum. His collecting activities involving numerous field expeditions to New Caledonia formed the taxonomic basis for this study.

Distribution and habitat. This species is known only from the southern portion of Grande Terre: localities range from Mt. Ouin on the north to Parc Provincial Rivière Bleue on the south (Fig. 79). Collection localities range from 700–1200 m el., with beetles collected via pyrethrin fog of trees and logs, hand collecting, and in a flight intercept trap into which one beetle was able to climb.

9. *Cyphocoleus miricollis* Fauvel, 1882

Figures 65, 73, 80, 89, 99

Diagnosis. This species shares the elongate prothorax with transversely wrinkled notum and acutely projected

front angles with *C. monteithi*, but the elytra are very flat, and the elytral striae distinctly punctate, the punctures expanding striae breadth (Fig. 99). The pronotum is narrowly trapezoidal, with broadly rounded hind angles and a deep transverse groove defining a broadly elevated pronotal basal margin, APW/BPW = 1.28–1.40. Based on the two examined specimens, it appears that this species carries a layer of environmental varnish similar to that observed for *C. monteithi* above (Fig. 85), not the abundant layer of environmental debris that coats individuals of *C. mirabilis*, *C. moorei*, and *C. lescheni* (Figs 100–103). Standardized body length 7.3–7.7 mm.

Description ($n = 2$). Head capsule ovoid with deeply constricted neck, genae distinctly incurved at back of head; frons with large, shallow chevron-shaped medial impression, frontal grooves broad and subparallel; eyes small, moderately convex, ocular ratio 1.30–1.50; supraorbital setae absent; mandibles moderately elongate, length $2.5 \times$ distance from antennal articulatory socket to anterolateral margin of labrum; gena glabrous. Pronotum narrow, tubular, MPW/PL = 0.63–0.67; median longitudinal impression deep, interrupting orientation of deep transverse wrinkles, terminated anteriorly as a deep pit; anterior marginal bead very broad, the deep groove just posterad bead interpreted as anterior transverse impression; proepipleuron and proepisternum bulging outward, visible in dorsal view for much of pronotal length, proepisternum smooth. Elytra broadly ellipsoid, MEW/EL = 0.68–0.69; humeri broadly angulate laterad depressed scutellum and parascutellar interval; parascutellar setae present, articulatory socket papillate, elevated above elytral surface; elytral striae deeply incised, punctate, the punctures separated by about $5 \times$ puncture diameter; elytral intervals distinctly convex, the sutural, third, fifth, and seventh interval subcarinate, most evidently so basally; dorsal elytral setae absent; lateral elytral margin straight to slightly concave laterad anterior series of lateral elytral setae; lateral elytral setae arranged as 6 + 6; subapical elytral seta present, apical seta absent; subapical sinuation distinctly concave, sinuation subangulately meeting lateral margin; elytral apices broadly rounded, margin deeply invaginated at fused suture. Mesepisternum impunctate; mesepisternum with dorsal length subequal to diagonal width. Abdomen of males and females with apical ventrite broadly, slightly concave medially; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs gracile, moderately long; metacoxae bisetose; tarsomeres relatively broad and short, mt1 length $0.21 \times$ tibial length; mt4 with long, broad apical lobes, length to apex of outer lobe $2.67 \times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture reduced, frons with surface shiny, transversely stretched isodiametric mesh traceable over portions of surface; pronotum glossy with fine transverse lines visible over portions of surface; elytral glossy on disc with transverse lines visible apically; body surface – head, pronotum, elytra, and ventral surfaces – with sparse pelage of very short setae (these setae may

be removed in part by cleaning). Coloration of head and pronotal disc rufopiceous; prothoracic ventrites piceous; elytra rufobrunneous; thoracic and abdominal ventrites rufopiceous, apical abdominal ventrite apically brunneous; femora and tibiae rufobrunneous, tarsi brunneous.

Male genitalia (n = 1). Male aedeagal median lobe robust, broadly parallel sided from base to apex of ostial opening, dorsoventral breadth at midlength 0.25× distance from tip to base of closed basal bulb (Fig. 89); lobe shaft slightly melanized, the internal sac visible through lobe wall in unverted position; lobe apex parallel-sided, dorsoventral breadth slightly longer than length; tip of lobe evenly rounded.

Female reproductive tract (n = 1). Bursa copulatrix broadly columnar, distance from base of gonocoxites to spermathecal basal sclerite 2.7× maximum breadth (dissection compressed under cover slip) (Fig. 65); bursal walls thin, translucent, the lumen smooth; basal gonocoxite with apical fringe of five setae (Fig. 73); apical gonocoxite broad basally, but narrow for much of length, with narrowly rounded apex and two lateral ensiform setae.

Types. Lectotype male (IRSN) hereby designated: M^t Mou (white label glued to larger pink label) Coll. R. I. Sc. N. B. / Nouvelle Calédonie / rec. / Deplanche / ex. coll. Fauvel // type (pink label with black border) // Coll. et det. A. Fauvel / *Cyphocoleus* 1882 / miricollis n. sp. / R. I. Sc. N. B. 17.479 // LECTOTYPE / *Cyphocoleus* / miricollis / Fauvel 1882 (black-bordered red label // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015.

Distribution and habitat. Known from sites in the southern mountains of Province Sud, near Mt. Ouin, at Mt. Mou, and at Forêt Nord (Fig. 80, Suppl. material 3).

10. *Cyphocoleus mirabilis* (Park & Will), comb. n.

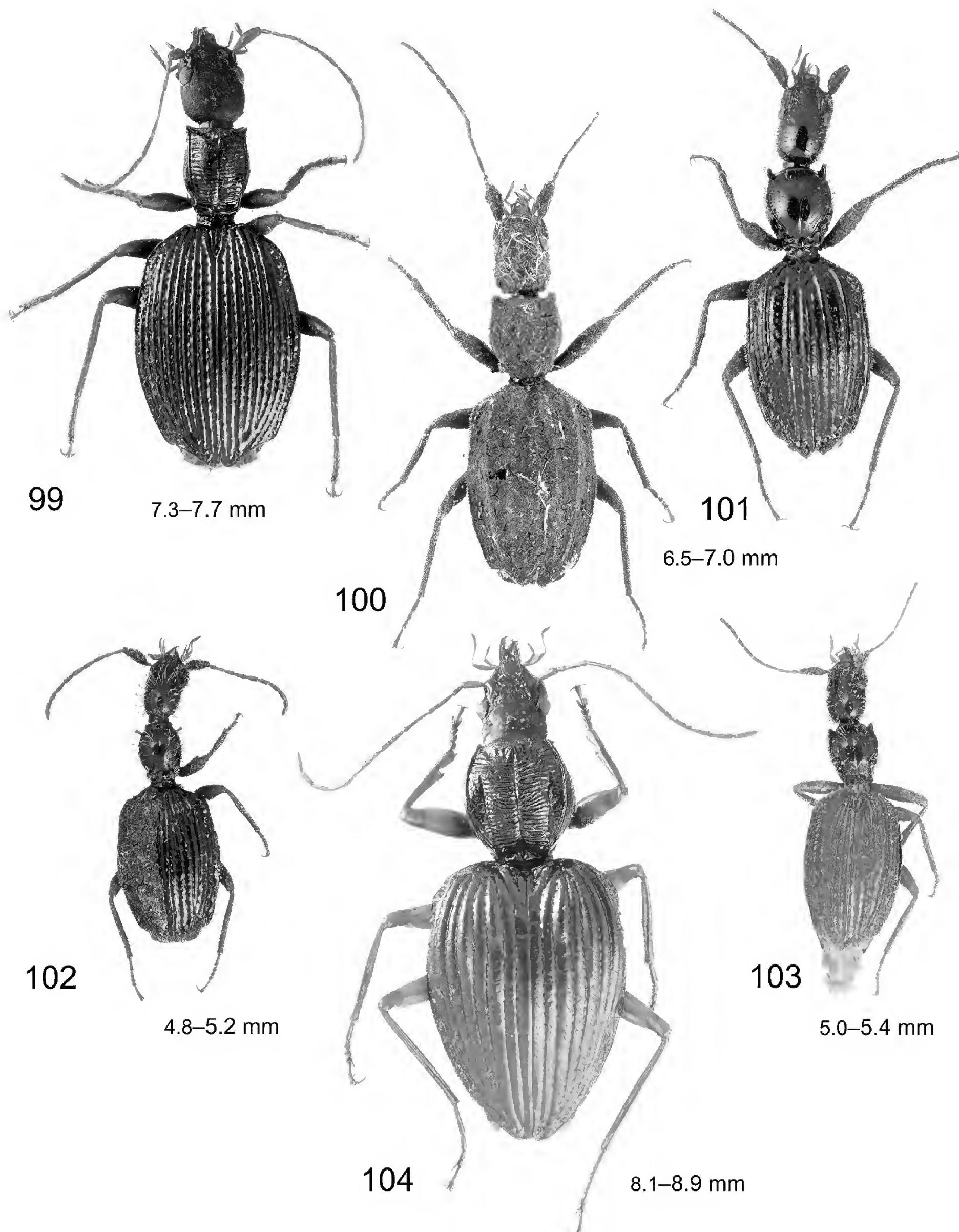
Atongolium mirabile Park & Will, 2008: 100.

Figures 30, 74, 81, 100–101, 105

Diagnosis. This species comprises one-third of a species triplet characterized by anterior and posterior projections on the front and hind angles of the pronotum (Figs 101–103), as well as presence of a pelage of setae that are club- or paddle-shaped: i.e. the setae are 2–3× broader apically than at their base. *C. mirabilis* is the largest-bodied of the three; standardized body length 6.5–7.0 mm, and also differs by the larger eye size: eyes slightly convex with 12 ommatidia present across a horizontal eye diameter. The apical abdominal ventrite bears a single seta on its apical margin in both males and females of this species, whereas females of the other two species in the triplet – *C. moorei* and *C. lescheni* – have two setae each side of the apical ventrite's apical margin. This species shares with *C. lescheni* the presence of a lateral marginal carina connecting the two pronotal processes, whereas *C. moorei* lacks such a carina. Conversely, dark rufous body coloration is shared among individuals of *C. mirabilis*

and *C. moorei* (Figs 101, 102) versus the pale brunneous and flavous coloration of *C. lescheni*.

Description (n = 3). Head capsule elongate, genae subparallel behind eyes and deeply converging at constricted neck; frons with small dimple-like depression medially between eyes, the dimple lined with isodiametric sculpticells; frontal grooves broad and deep, restricted to portion of frons anterad eyes; eyes small and slightly convex, a depressed groove continuous with groove at lateral edge of frons extended from eye dorsum to midpoint of eye hind margin; supraorbital setae absent; mandibles moderately elongate, length 2.0× distance from antennal articulatory socket to anterolateral margin of labrum; antennal scape broadly fusiform, length 3× maximal breadth; gena glabrous. Pronotum convex dorsally, with broadly spatulate processes at front and hind angles, the front processes flatter and broader in longitudinal orientation, the posterior processes more hornlike; lateral marginal carina extended and diminished behind posterior process, pronotal median base depressed but not margined; median longitudinal impression finely incised with surface sloping to meet at deepest portion; anterior transverse impression represented by oblique depressions that define an anterior pronotal collar about as wide as neck of head; proepipleuron and proepisternum bulging outward, visible in dorsal view in basal half of pronotal length; proepisternum smooth; prosternal process deeply depressed anterad procoxae, broadly depressed medially on ventral face, and depressed in an inverted “Y” pattern on posterior face resulting in a dorsomedial bump. Elytra only moderately convex overall, scutellum and sutural stria slightly depressed relative to stria 3; at midlength, sutural and fifth interval distinctly elevated, third interval slightly less so but it is also more elevated than intervals 2, 4, and 6; humeri very narrow, the basal groove present only from base of greatly elevated fifth interval to subangulate lateral margin just outside anterior series of lateral elytral setae; parascutellar and dorsal elytral setae absent; lateral elytral setae arranged 6 + 3 + 3, their articulatory sockets papillate, upraised above elytral surface: subapical elytral seta present, apical seta absent; subapical sinuation distinctly concave, the median portion of concavity upraised thereby elevating elytral margin; elytral apices tightly rounded, protruded, a deep invagination between them adjacent to the fused suture. Mesepisternum impunctate; metepisternal dorsal length subequal to diagonal width. Abdomen with very shallow, broad concavity medially on both male and female apical ventrite. Legs moderate, tarsomeres relatively short, mt1 length/tibial length = 0.21; mt4 length to apex of outer lobe 1.2× median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture absent on vertex except in median dimple; surface of pronotal and elytral disc glossy, indistinct transverse lines over portions of elytral surface; pelage of club-shaped setae well developed; setae on head capsule and pronotum moderately expanded, twice as broad apically as basally; setae broad and paddle-like on prothoracic lateral carina and anterior and posterior pronotal process-



Figures 99–104. Dorsal habitus photographs of *Cyphocoleus* spp.: **99**, *C. miricollis*, Forêt Nord; **100**, *C. mirabilis* female, environmental patina intact, Mt. Koghi; **101**, *C. mirabilis* male, environmental patina removed, Mt. Koghi; **102**, *C. moorei* female, environmental patina removed from forebody and right elytron, E. Table Unio; **103**, *C. lescheni* female, environmental patina removed, elytra reassociated with dissected specimen, Aoupinié; **104**, *C. fasciatus* male, teneral specimen lacking environmental patina, Mt. Panié.

es; elytra with broad paddle-like setae on sutural, third, and fifth intervals, setae narrower apically on intervals 2, 4, and 6; elytral lateral margin with short paddle-like setae, their length about half that of longer setae on odd intervals; ventral body surface and legs covered with dense pelage of short microsetae, the setae on legs more robust than those on ventrites. Coloration of head capsule dark rufous; antennal segments 1–4 rufobrunneous, outer antennomeres flavous with rufous cast; pronotum, elytra, and thoracic sclerites and abdominal ventrites dark rufous with a piceous cast; femora rufobrunneous, tibiae darker, rufopiceous, tarsi brunneous.

Male genitalia. Male aedeagal median lobe robust, broadly parallel sided in basal half, evenly tapered in distal half to subacuminate tip, dorsoventral breadth at midlength $0.22 \times$ distance from tip to base of closed basal bulb (Fig. 29); lobe apex elongate, evenly tapered to subacuminate tip, dorsoventral breadth $0.2 \times$ distance from distal margin of ostial opening to tip.

Female reproductive tract (n = 1). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite $2 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 105); bursal walls thin, translucent, lumen without spicules but bursal surface wrinkled in distal two-thirds; basal gonocoxite with apical fringe of six setae (Fig. 74); apical gonocoxite narrowly subtriangular with narrowly rounded apex and two lateral ensiform setae.

Type. Holotype male (MNHN): NEW CALEDONIA: 21°45'S, 166° 09'E, Ningua Reserve Camp, 1100 m, 12–13.xi.2001, C. Burwell & G. Monteith, pyrethrum, trees & logs, 8639 (not examined; identification based on female paratype (QMB) and non-type male (MNHW))

Distribution and habitat. Known from across the southern third of New Caledonia, from Col d'Amieu on the north to Rivière des Pirogues on the south (Fig. 81, Suppl. material 3). All recorded microhabitats include tree trunks and downed logs, with beetles collected using pyrethrin fog. The elongate paddle-shaped setae distributed over the body surface are associated with a thick layer of environmental patina (Figs 100, 101).

11. *Cyphocoleus moorei* (Park & Will), comb. n.

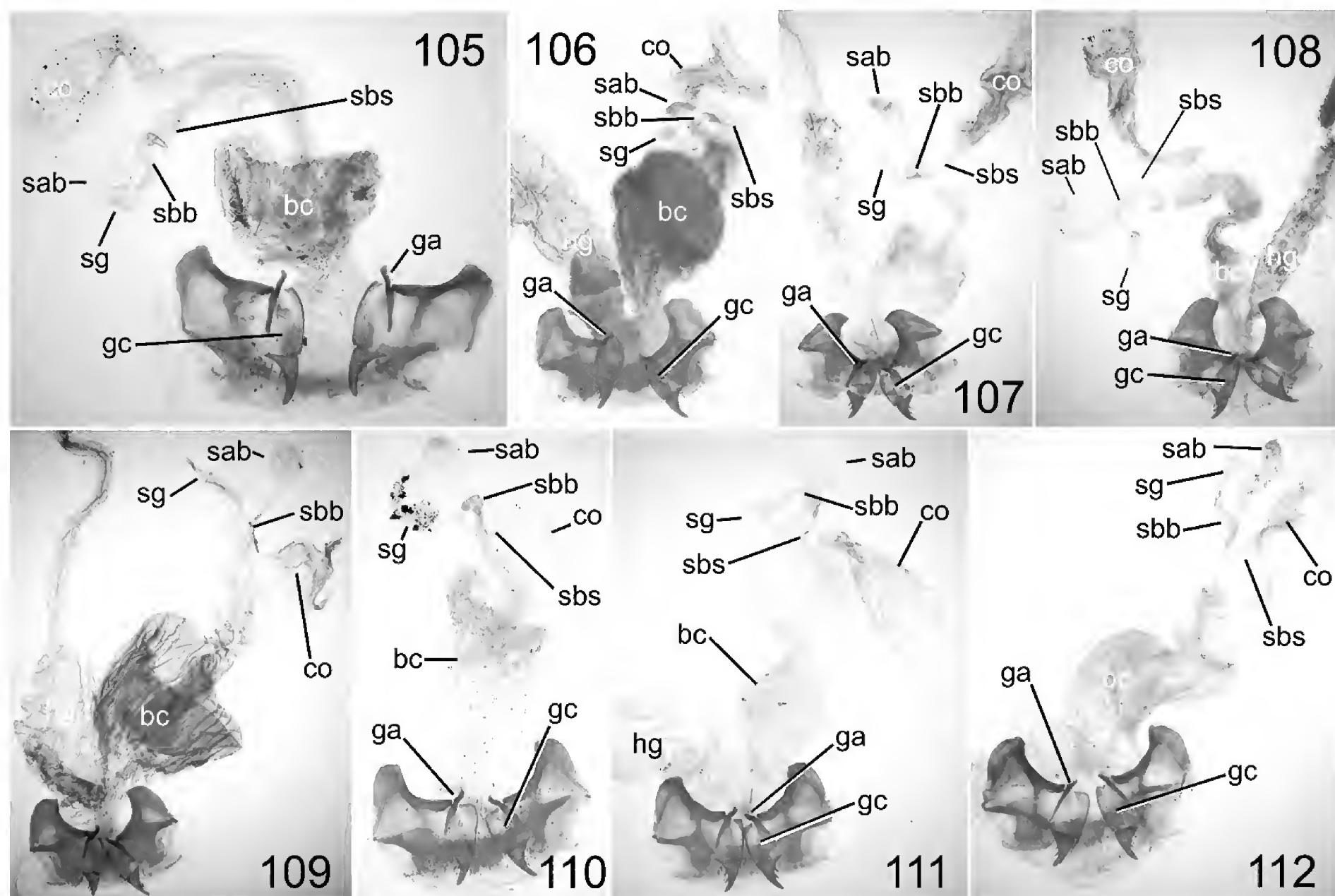
Atongolium moorei Park & Will, 2008: 101.

Figures 81, 102

Diagnosis. This second of the species triplet with anterior and posterior pronotal processes is unique in the absence of a lateral carina joining the processes, the pronotum fused to proepipleuron without any evidence of the shared suture (Fig. 102). The pronotal processes are both columnar, the anterior process half the height of the posterior, and both topped with a tuft of approximately nine club-shaped setae. The elytral intervals are distorted in this species, with the second interval absent basally due to convergence of the sutural and third intervals. Conversely, the fourth interval appears split basally, resulting

in the highly carinate fifth interval maintaining its fifth place position relative to the inner intervals throughout its length. The less convex sixth interval lies just laterad the carinate fifth interval, with the seventh interval very low and in part confused with the sequence of lateral elytral setae. The eyes of these beetles are very small in diameter, though slightly convex, with eight ommatidia horizontally across the diameter: the same ommatidial count as *C. lescheni* below. Standardized body length 4.8–5.2 mm.

Description (n = 2). Head capsule narrow elongate, genae parallel behind eyes, basally constricted to narrowly constricted neck (Fig. 102); frons depressed between the eyes relative to convex vertex; frontal grooves deep, broad, depressed mesad bases of antennae; supraorbital setae absent; mandibles moderately elongate, length $2.1 \times$ distance from antennal articulatory socket to lateroapical margin of labrum; antennae only moderately elongate, apical antennomeres filiform; scape greatly swollen, flattened dorsoventrally so that it assumes the profile of a cricket bat at midlength, scape length $2.3 \times$ maximal breadth; gena glabrous except for pelage, subgenal seta absent. Pronotum evenly ellipsoid in dorsal view, MPW/PL = 0.77; pronotal disc convex in both lateral and longitudinal dimensions, median base depressed relative to center of disc, with obsolete marginal bead defined by very shallow groove near margin; median longitudinal impression shallow, smooth, best defined by darker cuticle at deepest part; anterior transverse impression interpreted as deep transverse groove that defines upturned anterior collar; proepisternum bulging outward, visible in dorsal view, smooth; prosternal process broadly, medially depressed near front of procoxae, more narrowly depressed medially on ventral face, broadly medially depressed on posterior face. Elytra broad, moderately convex, little depressed laterally; scutellum depressed and basal margin medially inflexed at suture; humeri evenly sloped from scutellum to narrowly rounded margin just laterad front of anterior series of lateral elytral setae; parascutellar and dorsal elytral setae absent; fifth elytral interval subcarinate, more elevated than other moderately convex intervals; lateral elytral setae arranged as 6 + 3 + 3, their articulatory sockets papillate, upraised above surrounding cuticle; subapical elytral seta present, apical seta absent; subapical sinuation distinctly concave, most concave portion of sinuation convexly upraised; elytral apices broadly rounded, separated by moderate invagination centered on fused suture. Mesepisternum impunctate; mesepisternum with dorsal length $1.1 \times$ diagonal width. Abdomen of female with broad, shallow concavity medially, two setae each side. Legs moderately long, mt1 length/tibial length = 0.21; metacoxa bisetose; mt4 length to apex of outer lobe $1.2 \times$ median length, 4–5 ventrolateral setae each side. Microsculpture of head absent, frons and vertex glossy; pronotal disc and lateral sclerites glossy; elytra without microsculpture on higher portions of intervals, fine transverse lines traceable in deeper portions of striae and punctures; head and pronotum with pilose pelage of elongate club-shaped setae; pronotal processes with tufts of pad-



Figures 105–112. Female reproductive tract, ventral view, for *Cyphocoleus* spp.; **105**, *C. mirabilis*, Mt. Koghi; **106**, *C. fasciatus*, Mt. Panié; **107**, *C. cychroides*, Pic d'Amoa; **108**, *C. latipennis*, Mt. Panié; **109**, *C. cardiopterus*, Mt. Mou; **110**, *C. globulicollis*, Col des Roussettes; **111**, *C. flavipes*, Nouméa; **112**, *C. subulatus*, Forêt de Thi. For abbreviations see Table 1.

dle-like setae at apices; elytral intervals lined with series of paddle-like setae of length similar to tufts on pronotal processes; elytral margin lined with very short paddle-like setae; ventral surfaces of head, thorax, and abdomen covered with sparsely distributed pelage of short microsetae, with similar-lengthed setae covering anterior surfaces of femora, dorsal surfaces of tibiae; tarsomeres setose dorsally, the setae arranged in two dorsolateral longitudinal series. Coloration of head, prothorax, elytra, and thoracic and abdominal ventrites rufous; antennal scape dark, rufopiceous, outer antennomeres 2–11 brunneous; femora rufoflavous, tibiae and tarsomeres brunneous.

Male genitalia. Male aedeagal median lobe robust, broadly parallel sided in basal half, ventral margin slightly convex near midlength, dorsoventral breadth at midlength $0.2 \times$ distance from tip to base of closed basal bulb (Park and Will 2008; Fig. 3K); lobe apex tapered to sub-acuminate, slightly downturned tip, dorsoventral breadth $0.25 \times$ distance from distal margin of ostial opening to tip.

Female reproductive tract. Not examined (see Park and Will 2008).

Type. Holotype male (MNHN): NEW CALEDONIA, $21^{\circ}45'S$, $166^{\circ}09'E$, Ningua Reserve Camp, 1100 m, 12–13.xi.2001, C. Burwell & G. Monteith, pyrethrum, trees & logs, 8639 (not examined; identification based on female paratype (QMB)).

Distribution and habitat. Known from slightly north of the distribution of *C. mirabilis* along the Sarraméa-Canala Road near Table Unio, though with a broad sympatric overlap with that species ranging from Col d'Amieu to Ningua Reserve (Fig. 81, Suppl. material 3). Specimens have been found in leaf litter, and by pyrethrin fogging of trees and logs. The elongate club-shaped setae over the body surface are associated with a 0.2 mm thick environmental patina incorporating plant-based detritus (Fig. 102).

12. *Cyphocoleus lescheni* sp. n.

<http://zoobank.org/D211D53A-BC34-491B-A11A-DDF3D4A36DB6>
Figures 75, 81, 103

Diagnosis. Among the triplet of species with setose pronotal processes, *C. lescheni* can be diagnosed by: **1**, presence of a carinate ridge between the anterior and posterior pronotal processes; **2**, small, flat eyes, eight ommatidia crossed on a horizontal diameter; **3**, elytra with seventh interval the most carinate, its convexity marking the border between a moderately flat disc bearing six intervals, and a much more vertical elytral margin with a pelage-seta bearing eighth interval. Standardized body length 5.0–5.4 mm.

Description (n = 2). Head capsule elongate, genae parallel behind eyes, basally constricted to well-defined neck; frons convex between eyes, frontal grooves linear and moderately convergent anterad, widest at frontoclypeal suture; supraorbital setae absent; mandibles moderately elongate, length 1.9× distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, apical antennomeres filiform; scape fusiform, broadened into a paddle-like shape, length 2.5× maximal breadth; gena glabrous except for pelage, subgenal seta absent. Pronotum orbicular; anterior pronotal process short, apically obtuse, the process flattened longitudinally; posterior pronotal process columnar, peg-like, slightly more than twice as long as broad; lateral ridge joining two process a low rounded carina; pronotal median base constricted, surface undulated with median and two lateral depressions separate by low rounded longitudinal ridges, lateral depressions bordering outside by similar low, rounded lateral longitudinal ridges; median longitudinal impression finely incised, moderately deep; anterior transverse impression interpreted as a punctulate transverse groove that defines a rounded anterior collar, the collar broadest medially, terminated laterally anterad pronotal processes; proepipleuron and proepisternum bulging outward, visible in dorsal view; proepisternum smooth; prosternal process medially concave anteriorly near front of procoxae, deeply medially depressed on ventral face, broadly depressed medially on posterior face. Elytra narrow, elongate, with scutellum and parascutellar interval depressed relative to very carinate seventh interval, the carination of that interval greatest at base; parascutellar and dorsal setae absent; humeri extended anterad at base of seventh interval, basal margins straight and narrowly diverging posterad humeral angle to position laterad anterior three lateral elytral setae where the margins become subparallel posteriorly; lateral elytral setae arranged as 6 + 3 + 4, the setal articulatory sockets papillate, raised as mounds above the surrounding cuticle; subapical elytral seta present, apical seta absent; subapical sinuation distinctly concave, margin upraised at middle of concavity, the sinuation subangulately meeting lateral margin. Mesepisternum impunctate; metepisternal dorsal length 1.3× diagonal width. Abdomen with apical margin of apical ventrite moderately concave medially in females, the middle pair of the four apical setae just laterad median concavity. Legs moderately elongate, gracile; mt1 length/tibial length = 0.21; mt4 length to apex of outer lobe 1.2× median length, with 4–5 ventrolateral setae each side. Microsculpture of head and pronotal disc glossy, without microsculpture; elytral disc with intervals glossy, indistinct isodiametric (?) sculpticells in deepest portions of striae; pelage well developed, comprising club-like to paddle-like setae; head capsule densely covered with club-like setae that are longest on posterior portion of head capsule, about half a long on frons, and very short, scale-like anterad and below eyes; pronotal disc pelage consisting of setae much like present on posterior portion of head, pronotal processes and lateral ridges with

apically broader, more paddle-like setae; elytral intervals lined with longitudinal series of club-like setae, the setae broader apically on odd intervals (sutural, 3, 5, 7), and shorter and narrower apically on even intervals; elytral lateral margin densely lined with short, thick setae; ventral body surface, femora and tibiae covered with very fine, apically narrowed microsetae; tarsomeres with additional paired dorsolateral setae, four on mt1 and two on mt2–4. Coloration of head and pronotal disc rufous, pronotal lateral ridge somewhat darker due to deeper cuticle; elytra and abdominal ventrites rufoflavous, elytral lateral margin dark rufous (as in pronotal lateral carina); legs flavous.

Female reproductive tract (n = 1). Basal portion of one right gonocoxa available for study; basal gonocoxite with apical fringe of five setae; apical gonocoxite apparently subtriangular based on basal fragment, with two lateral ensiform setae.

Types. Holotype female (EMEC deposited in MNHN) (body pointed, fused elytra mounted on platen): NEW CALEDONIA, Prov. / Nord L'Aoupinié 24-iii-2007 / R. Leschen rotten wood / berlesate NC076 800m el. / 21°11'S/165°17'E // UC Berkeley / EMEC / 1137861 (plicated bar code) // *Cyphocoleus* revision / measure specimen 1 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / lescheni / J. K. Liebherr 2016 (black-border red label).

Paratype female (EMEC): Aoupinié, 800 m el., 21°11'S, 165°17'E, Berlesate rotten wood, 24-iii-2007, Leschen.

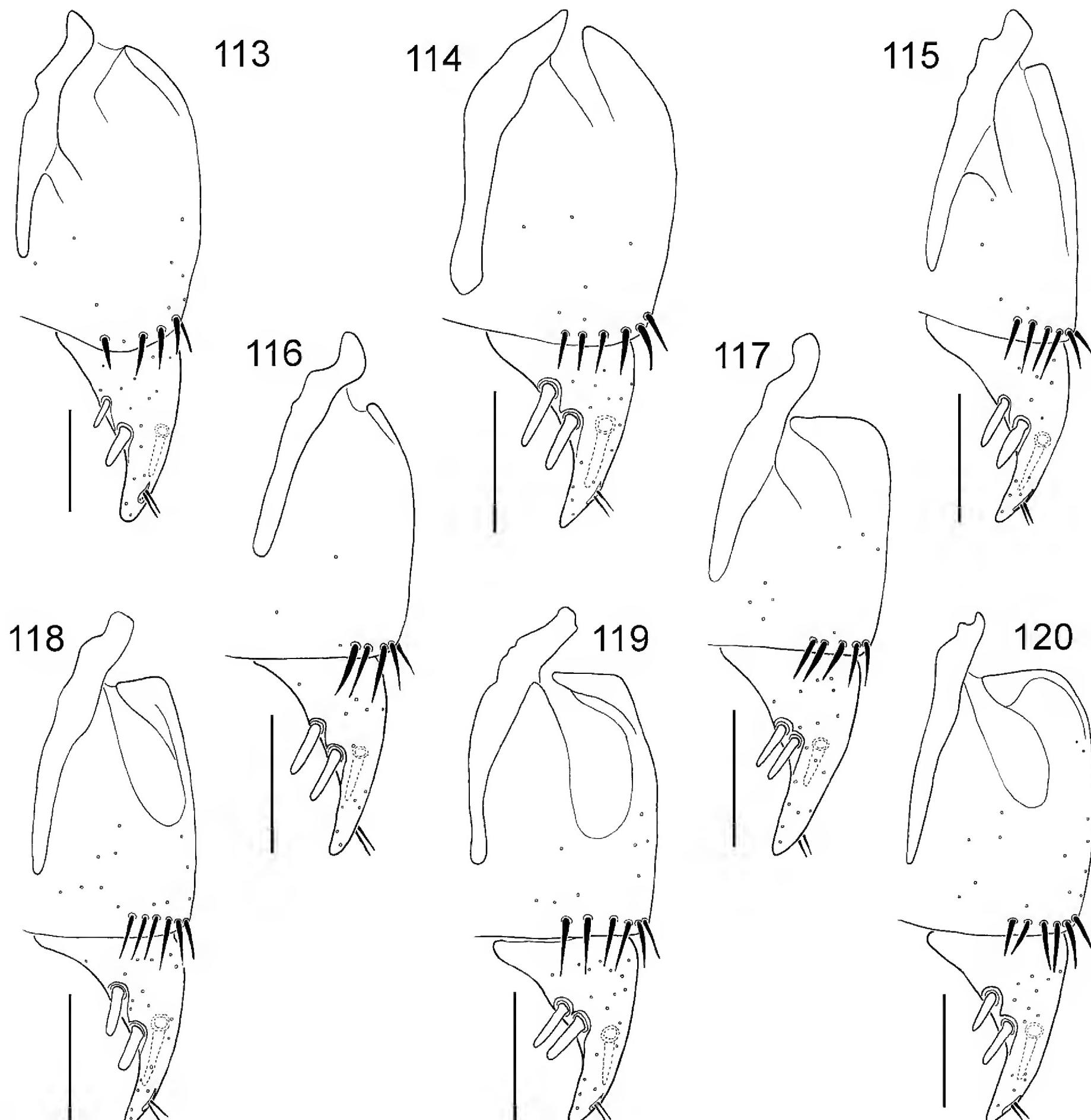
Etymology. We take great pleasure in naming this species for Dr. Richard A. B. Leschen, Curator, New Zealand Arthropod Collection and the collector of the two type specimens currently representing this species. Dr. Kipling W. Will is accorded author status based on his recognition of this species as undescribed from amongst the material collected during the 2007 New Zealand Arthropod Collection-University of California, Berkeley Essig Museum expedition.

Distribution and habitat. Both types of this species were collected from leaf litter by Berlese extraction. The long club-shaped setae afford the means for a thick layer of environmental patina to adhere to the body surface.

13. *Cyphocoleus fasciatus* sp. n.

<http://zoobank.org/C0597858-AACC-475B-BEA4-DE5CD75E2B35>
Figures 80, 90, 104, 106, 113

Diagnosis. This species (Fig. 104) comprises beetles of largest body size – standardized body length 8.1–8.9 mm – among those species characterized by orbicular pronota and broadly ovate, inflated elytra (Figs 121–125, 161–164). Indeed, *C. fasciatus* is the adelphotaxon to those taxa (Figs 44–46). Additionally, individuals of *C. fasciatus* exhibit legs with banded femora, their smoky piceous basal halves and subapical band contrasted to flavous bands in the apical half and at the apex (Fig. 104). The pronotal disc is distinctly transversely



Figures 113–120. Female right gonocoxae, ventral view, for *Cyphocoleus* spp. illustrating apical fringe setae of basal gonocoxite 1, and two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae on apical gonocoxite 2; **113**, *C. fasciatus*, Mt. Panié; **114**, *C. cycloides*, Pic d'Amoa; **115**, *C. latipennis* Mt. Panié; **116**, *C. cordatus*, Forêt Nord; **117**, *C. globulicollis*, Col des Roussettes; **118**, *C. flavipes*, Nouméa; **119**, *C. bourailensis*, Bourail; **120**, *C. subulatus*, Forêt de Thi. Scale bar, 0.10 mm.

wrinkled, with longitudinal parasagittal impressions defining a central disc and lateral flanges extended to the lateral marginal bead. As in the three preceding species – *C. mirabilis*, *C. moorei*, and *C. lescheni* (e.g. Fig. 100) – individuals of this species are capable of developing a very thick environmental patina that obscures their dorsal body surface under deep, anastomosing layers of debris derived from leaf litter and humus. In keeping with those species, and indicative of a proximal phylogenetic relationship, the lateral marginal ridge of the pronotum terminates posteriorly in a projection: in this species a stout, obtuse tooth.

Description ($n = 5$). Head capsule broad, stout, genae parallel behind convex, pop-eyed compound eyes; neck constriction broad, moderately deep dorsally but not evidenced laterally; ocular ratio 1.39–1.45, eyes with 20 ommatidia across horizontal diameter; frons medially rugose between eyes, frontal grooves distinctly doubled, the deep canaliculi separated by a distinct rounded ridge, groove convergent to frontoclypeal suture; supraorbital setae absent; mandibles moderately elongate, length $2.1 \times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae elongate, scape length $2.9 \times$ maximal breadth; gena setose, subge-

nal seta present. Pronotum orbicular, front angles briefly but acutely projected; lateral marginal bead subcarinate, elevated, terminated posteriorly in blunt, obtuse tooth that continues medially as a diminished basal marginal bead, though median base not marginated; pronotal base constricted, set off from disc by median and two oblique lateral depressions; median longitudinal impression deep, moderately broad, undulated longitudinally with transverse wrinkles of disc not all aligned across impression; anterior transverse impression represented by an oblique series of longitudinal depressions that extend anterad at their ends as two to three longitudinal canaliculi crossing the anterior callosity; two linear parasagittal impressions present, these grooves extended from basal tooth $\frac{3}{4}$ pronotal length toward front angles; pronotal flanges laterad parasagittal impressions irregularly wrinkled, surface smoother than median pronotal disc; proepipleuron and proepisternum bulging outward, visible in dorsal view; proepisternum irregularly and obliquely wrinkled, the wrinkles oriented more or less longitudinally; prosternum rugose, the surface with deep, irregular wrinkles that are most distinct near anterior margin; prosternal process distinctly marginated anteriorly by ridges surrounding procoxal cavities, broadly medially depressed on ventral face, narrowly carinate dorsally on posterior face. Elytra ovoid, disc elevated relative to depressed lateral margins, appearing somewhat cordate due to basal elevation of third to seventh intervals versus depressed scutellum and parascutellar interval; parascutellar seta present, situated at base of sutural interval, elevated on papillate articulatory socket; basal groove broadly rounded laterad depressed and inflexed scutellum; sutural, and elytral intervals 2, 4, and 6 moderately convex on disc, intervals 3, 5, and 7 elevated, subcarinate basally, the intervals broader where they are more convex; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7; subapical elytral seta present, apical seta absent; subapical sinuation well developed, concavity near lateral margin of sinuation extended ventrad to subangulately meet lateral margin, thus apical elytral margin not elevated inside sinuation; elytral apices broader rounded, separated by inflexed margin adjacent to fused suture. Mesepisternum impunctate, metepisternal dorsal length $0.9 \times$ diagonal width; metasternum with deep, laterally ovoid median fossa at base of metasternal process. Abdomen with broad, shallow medial concavity at apex of apical ventrite in both males and females; males with one seta each side of apical ventrite, females with two setae. Legs elongate, gracile; metacoxae bisetose; mt1 length/tibial length = 0.27; mt4 length to apex of outer lobe $2.33 \times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture of head stretched isodiametric mesh, visible over portions of vertex, microsculpture obscured in rugose area of frons and in frontal grooves; pronotal disc glossy, indistinct sculpticells traceable only in deepest portions of wrinkles; elytral disc glossy, obsolete transverse lines visible over portions of apex; sparsely distributed pelage of short microsetae visible on head capsule, prothorax, meso- and

metasternum, and coxae; elytra with pelage of microsetae arranged in mediolongitudinal series along elytral intervals; legs sparsely covered with very short, fine microsetae in addition to the larger fixed setae, these short setae also arranged in irregular longitudinal series on the dorsal surfaces of tibiae and tarsomeres. Coloration (specimen clear of environmental patina is teneral; Fig. 104) generally piceous on head capsule, prothorax, elytra, and meso- and metathorax; elytral epipleura narrowly dark rufous dorsally; abdominal ventrites rufopiceous, apical ventrite rufoflavous marginally; femora with distinct flavous bands in apical half and at apex that contrast greatly with the piceous coxae, dark rufous trochanters, and smoky brunneous tibiae and tarsi.

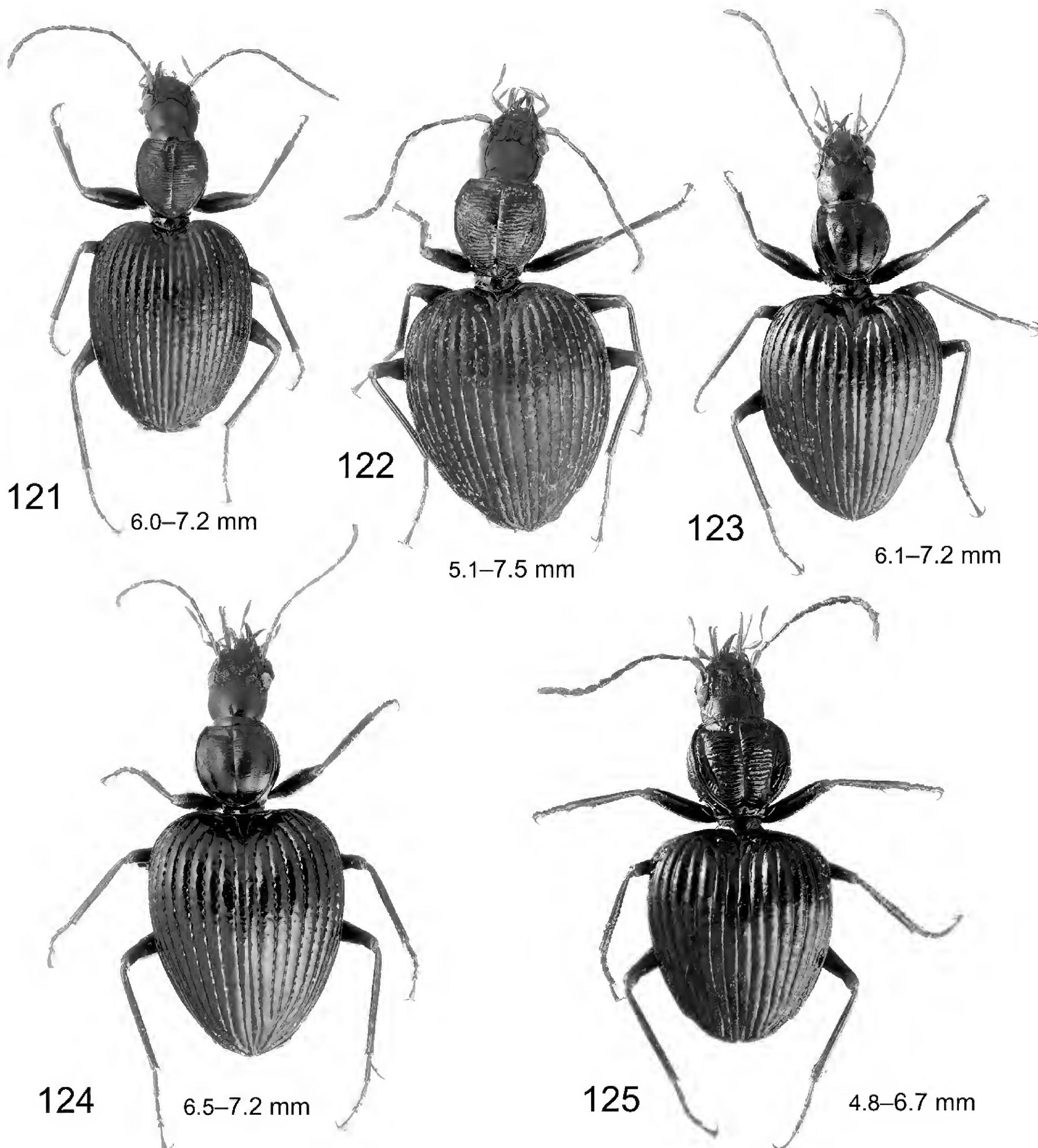
Male genitalia (n = 2). Male aedeagal median lobe robust basally, broadly parallel sided in basal half, evenly tapered in distal half to extremely elongate, curved, proboscis-like apex, dorsoventral breadth at midlength $0.16 \times$ distance from tip to base of closed basal bulb (Fig. 90); lobe apex extended beyond ostial opening in a broad curve, tip tightly rounded, dorsoventral breadth at midlength of apical extension $0.13 \times$ distance from distal margin of ostial opening to tip; sac with microtrichia, but without any heavily sclerotized structures.

Female reproductive tract (n = 1). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite $1.5 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 106); bursal walls thick, wrinkled, heavily stained with Chlorazol Black, luminal surface smooth; basal gonocoxite with apical fringe of five setae (Fig. 113), one very small on left gonocoxite; apical gonocoxite subtriangular with narrowly rounded apex and two lateral ensiform setae.

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA / $20^{\circ}34'S$, $164^{\circ}46'E$ / Mt Panie refuge, 1300 m / 16–18 Nov 2000. Bouchard / Burwell & Monteith. **9938** // QUEENSLAND / MUSEUM LOAN / DATE: Nov. 2003 / No. LEN 1688 (green label) // male habitus photo 1 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / *fasciatus* / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (26 specimens). NEW CALEDONIA: Mt. Panié, 950–1300 m el., $20^{\circ}34'S$, $164^{\circ}46'E$, 14–16-v-1984, Monteith & Cook (QMB, 1), refuge, 1300 m el., $20^{\circ}34'S$, $164^{\circ}46'E$, 16–18-xi-2000, Bouchard, Burwell & Monteith (QMB, 10; lot no. 9938), 08–09-xi-2001, Burwell (QMB, 2; lot no. 8764), below Maruia refuge, 1300–1350 m el., 25-xi-2010, Wanat & Ruta (MNHW, 1), 1300–1600 m el., $20^{\circ}35'S$, $164^{\circ}46'E$, 15-v-1984, Monteith & Cook (ANIC, 2; QMB, 4), E trail, 1350–1600 m el., rainforest, 24-xi-2010, Wanat & Ruta (MNHW, 1), summit, 1600 m el., $20^{\circ}35'S$, $164^{\circ}46'E$, 09-xi-2001, Burwell (QMB, 3; lot no. 8769), 18-xi-2000, Bouchard, Burwell & Monteith (QMB, 2; lot no. 9939).

Etymology. The species epithet *fasciatus* is derived from the Latin to “envelop with bands (Brown 1956)”, referring to the banded pigmentation of the femora of beetles comprising this species (Fig. 104).



Figures 121–125. Dorsal habitus photographs of *Cyphocoleus* spp., environmental patina removed: 121, *C. cychroides* male, Tionaki Tal; 122, *C. latipennis* male, Mt. Panié; 123, *C. cordatus* female, Forêt Nord; 124, *C. cardiopterus* female, Mt. Mou; 125, *C. globulicollis* female, Col des Roussettes.

Distribution and habitat. This species is known only from Mt. Panié at elevations ranging 950–1600 m (Fig. 80). Given the well-developed environmental patina borne by beetles of this species, they come in contact with ground litter during their activities. The well-developed pelage of microsetae on the dorsal body surface and prothoracic ventrites is associated with deep layers of environmental patina.

14. *Cyphocoleus cychroides* Chaudoir, 1877

Figures 107, 114, 121, 137

Diagnosis. Among all the smaller-bodied species with orbicular pronotum and cordate elytra (Figs 121–125, 161–164), this species stands out due to the narrowly orbicular pronotum, MPW/PL = 0.88–0.94, and pronotal disc that is evenly traversed by wrinkles but without longitudinal parasagittal impressions. The pronotal later-

al marginal beads arcuately extend to the narrow median base (Fig. 121). Some individuals of *C. latipennis* have the pronotum nearly as narrow, MPW/PL = 0.92–1.07, but beetles comprising *C. cychroides* differ by their lack of supraorbital setae, whereas *C. latipennis* is characterized by presence of the posterior seta, though it is located well behind the eye just anterad the constricted neck. The pronotal disc of *C. latipennis* also differs by the presence of parasagittal impressions, and median pronotal base not arcuately and continuously margined as in *C. cychroides*. Standardized body length 6.0–7.2 mm.

Description (n = 5). Head capsule narrowly ovoid, genae gradually narrowed to moderately constricted neck; eyes only slightly convex, oriented toward upper surface of head, ocular ratio quite variable, 1.20–1.56, about 18 ommatidia across horizontal diameter of eye; frons with paired, longitudinal depressions that surround a low median ridge; frontal grooves broad, deep, parallel, extended from just anterad hind margin of eye onto clypeus; mandibles elongate, length 2.1× distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length 2.75× maximal breadth; gena setose, subgenal seta present. Pronotum with front angles rounded, only slightly protruded; median base continuously margined, but bead straight along base; median longitudinal impression finely incised, slightly irregular as it traverses transverse wrinkles; anterior transverse impression a deep, oblique depression, defining a flat anterior callosity with indistinct longitudinal wrinkles; proepisternum slightly extended beyond marginal bead, narrowly visible in dorsal view; proepisternum mostly smooth, with indistinct vertical wrinkles; prosternal process broadly, medially depressed anteriorly, with paired, shallow longitudinal depressions ventrally, posterior face broadly convex. Elytra broadly cordate, basal groove sinuously incurved near depressed scutellum, continued in broad curve laterally around humerus, a slight hitch in the curve near base of third stria; discal intervals moderately convex, all intervals of subequal convexity; elytral striae deep, punctate, the punctures larger basally where they expand striae breadth; parascutellar seta present, articulatory socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller; subapical sinuation well developed, lateral portion of concavity joined to depressed lateral margin in broad curve; elytral apices conjoined, no invagination of apical margin at fused suture. Mesepisternum impunctate; metepisternal dorsal length 1.1× diagonal width; metasternum with broad, shallow median fossa at base of metepisternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.27; mt4 length to apex of outer lobe 1.6× median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture on vertex stretched isodiametric mesh, the

head capsule glossy; pronotal disc with evident transverse mesh visible within transverse wrinkles, the surface matte; elytral intervals covered with transverse-line microsculpture resulting in silvery iridescence; pelage little developed, glossy head capsule glabrous, pronotum and elytra with sparse distribution of exceedingly short microsetae, visible only in lateral view; ventrites and legs glabrous except for macrosetae. Coloration of body dorsum piceous, mouthparts, scutellum, and apical elytral margin rufopiceous; body venter including elytral epipleura rufopiceous; femora dark rufous; tibiae piceous medially, rufoflavous at base and apex; tarsi rufoflavous.

Male genitalia (n = 10). Male aedeagal median lobe robust, broadly parallel sided over basal 2/3 of length, the lobe shaft angled ventrally ventral ostial opening, dorsoventral breadth at midlength 0.20–0.25× distance from tip to base of closed basal bulb (Figs 91–98); lobe apex sinuously curved, tip may be knob-like with a constriction distad ostial opening (Figs 91, 92) or abruptly narrowed distad ostial opening to a parallel-sided apex (Figs 93–98); internal sac membranous without melanized microtrichia, length slightly greater than breadth (Figs 91, 93, 94, 96). Although the male aedeagi of individuals assigned to *C. globulicollis* exhibit substantial variation in the configuration of the apex, all of this variation is exhibited among individuals from the same well-sampled site; Mandjélia. All individuals from this site share other external attributes, as well as the subangulate apex to the aedeagal median lobe, and so this variation is interpreted as infraspecific.

Female reproductive tract (n = 2). Bursa copulatrix vase-shaped, abruptly narrowed distally near spermatheca, distance from base of gonocoxites to spermathecal basal sclerite 3× maximum breadth (dissection compressed under cover slip) (Fig. 107); bursal walls thin, translucent, luminal surface smooth; basal gonocoxite with apical fringe of five to six setae (Fig. 114); apical gonocoxite broadly triangular with pointed apex and two lateral ensiform setae.

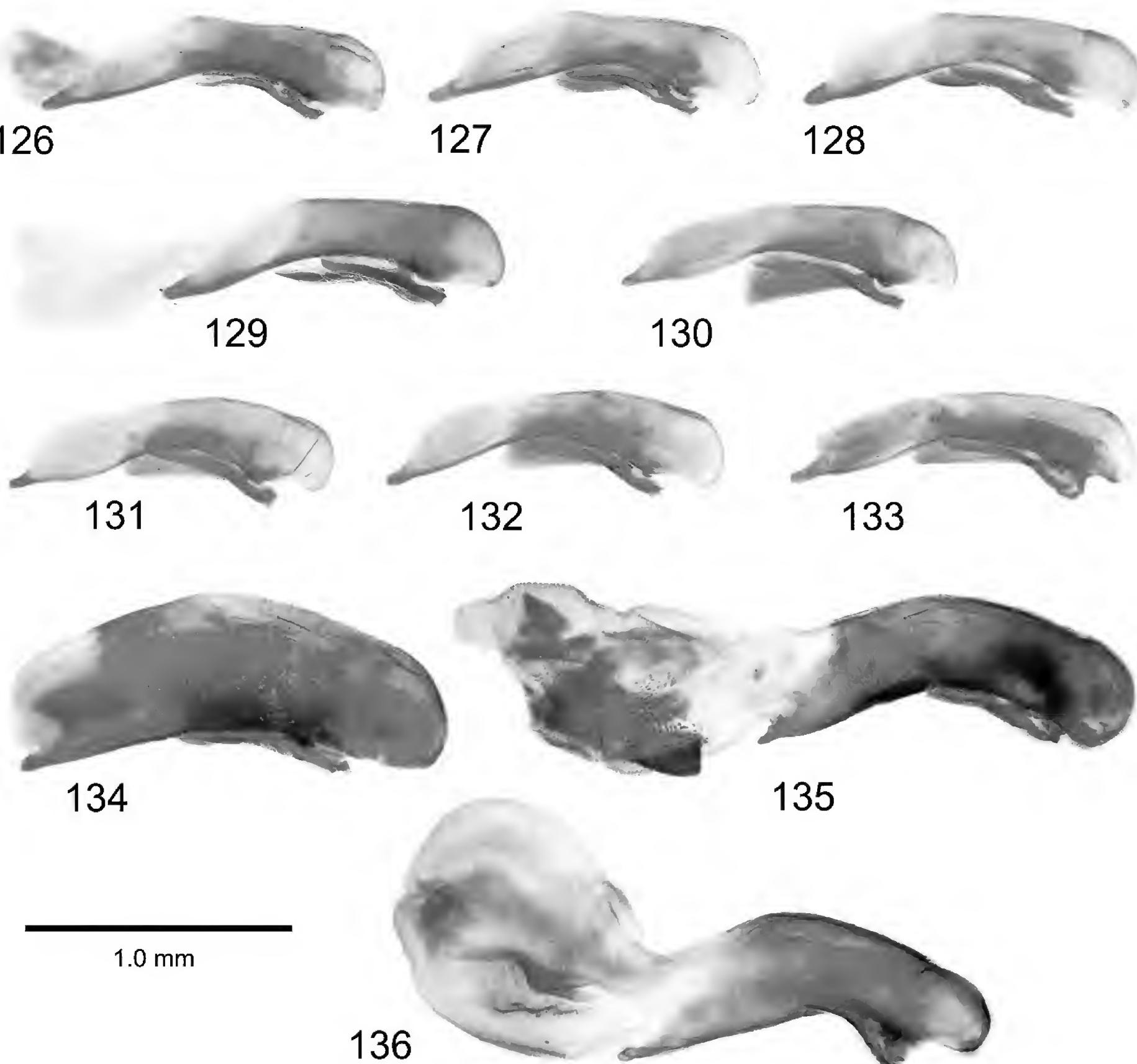
Types. Holotype male (MNHN): Ex Musæo / Chaudoir (red-inked white label with red border) // HOLOTYPE / *Cyphocoleus* / *cychroides* / Chaudoir 1877 (black-bordered red label). Holotype status is based on Chaudoir's (1877: 197) statement: "Il m'a été vendu par H.M. Deyrolle." Mandjélia summit, 750 m el. hereby designated type locality.

Distribution and habitat. Known from Province Nord. The recorded distribution is bounded by Canala on the south, and Col d'Amoss along the northeastern coast (Fig. 137, Suppl. material 3). Beetles have been collected from logs and trunks via the application of pyrethrin fog.

15. *Cyphocoleus latipennis* Fauvel, 1882

Figures 33, 108, 115, 122, 126–133, 138

Diagnosis. This species is characterized by presence of the posterior supraorbital seta, a configuration shared,



Figures 126–136. Male aedeagal median lobe and associated parameres of *Cyphocoleus* spp., dextral view: 126–133, *C. latipennis*; 126, internal sac everted, Mandjélia; 127–128, Mandjélia; 129, Mt. Panié; 130, Pic d'Amoa; 131–132, Aoupinié; 133, Ouenarou; 134–135, *C. cordatus*; 134, Mt. Koghi; 135, *C. cordatus*, internal sac everted, Forêt Nord; 136, *C. cardiopterus*, Dzumac Rd. jct.

among the nine *Cyphocoleus* species with orbicular pronotum and cordate elytra (Figs 121–125, 161–164), only with *C. subulatus* and *C. iledespinsensis*. This supraorbital seta is not close to the eye, but positioned far back on the head capsule close to the constricted neck. *C. latipennis* deviates from the other two species in exhibiting a very glossy vertex and glossy to transversely lined elytral intervals, versus a vertex covered with isodiametric sculpticells, and elytra with evident transverse-mesh microsculpture, best evidenced in the strial depressions. Standardized body length 5.1–7.5 mm.

Description ($n = 5$). Head capsule narrowly ellipsoid, genae gradually narrowed to moderately constricted neck; eyes only slightly convex, ocular ratio 1.46–1.53, 13–18 ommatidia across horizontal diameter of eye; frons with paired, elongate-ellipsoid depressions that surround a nar-

row elevated median carina; frontal grooves deepest and broadest just mesad eyes, sinuously convergent toward clypeus; mandibles elongate, length $2.3 \times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length $2.75 \times$ maximal breadth; gena setose, subgenal seta present. Pronotum with front angles rounded, slightly protruded; median base depressed relative to disc, lateral margin sinuate anterad median basal margin that is straight across base; median longitudinal impression deep, broad, extended to anterior margin; anterior transverse impression defined by shallow groove where discal wrinkles terminate, anterior callosity crossed by numerous longitudinal wrinkles; proepisternum extended beyond marginal bead, visible in dorsal view, smooth; prosternal process broadly, medially depressed anteriorly and on ventral face, narrowly

carinate posteriorly. Elytra broadly ovoid, depressed mediobasally between parascutellar setae; basal groove subangulate basad sutural stria, lateral margin broadly and evenly extended outside humeral angle; discal intervals moderately convex, all intervals of subequal convexity; elytral striae deep, punctate, the punctures limited at the deepest portion of strial depression (and so easy to miss in uncleared specimens); parascutellar seta articulatory socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller; subapical sinuation moderately developed, lateral portion of concavity joined to depressed lateral margin in broad curve; elytral apices conjoined, no invagination of apical margin at fused suture. Mesepisternum impunctate; metepisternal dorsal length $1.0 \times$ diagonal width; metasternum with broad, shallow median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.27; mt4 length to apex of outer lobe $1.8 \times$ median tarsomere length, 3–4 ventrolateral setae each side. Pelage little developed, glossy head capsule, pronotum, and elytra with only sparsely distributed, very short microsetae, visible only in lateral view; pro-, meso-, and metasternum with evident pelage of microsetae, the setae longer than on dorsal surface; second and third abdominal ventrites with short, sparse microsetae medially, other ventrites and legs glabrous except for macrosetae. Coloration of body dorsum piceous, mouthparts rufopiceous; ventral surfaces of head and prothorax and thoracic sternites piceous, elytral epipleuron and abdominal ventrites to rufopiceous to dark rufous; femora dark rufous except for paler, rufoflavous apex, tibiae and tarsi rufobrunneous.

Male genitalia (n = 14). Male aedeagal median lobe gracile, median lobe constricted near midlength, dorsoventral breadth at midlength $0.13\text{--}0.16 \times$ distance from tip to base of closed basal bulb (Figs 126–133); lobe apex variously tapered to parallel sided basad broadly (Figs 128, 129) to narrowly rounded (Figs 126, 127, 130–133) tip; internal sac membranous without melanized microtrichia, length $2 \times$ breadth (Fig. 129).

Female reproductive tract (n = 3). Bursa copulatrix narrowly elongate, distance from base of gonocoxites to spermathecal basal sclerite $7 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 108); bursal walls thin, translucent, luminal surface smooth except for thin band of very fine setae at midlength; basal gonocoxite with apical fringe of five to six setae (Fig. 115); apical gonocoxite subtriangular with pointed apex and two lateral ensiform setae.

Types. Holotype female (IRSN): Nelle. Calédonie (white label glued to larger pink label) Coll. R. I. Sc. N. B. / Nouvelle Calédonie / rec. / De- / planche / ex. coll. Fauvel // type (pink label with black border) // Coll. et det. A.

Fauvel / *Cyphocoleus* / latipennis Fauv. // HOLOTYPE / *Cyphocoleus* / latipennis / Fauvel 1882 (black-bordered red label. Fauvel (1882: 250) wrote: "je presume qu'il a été pris au Mont Mou", with this locality considered the type locality.

Distribution and habitat. This is the most broadly distributed *Cyphocoleus* species, distributed along the length of Grande Terre (Fig. 138, Suppl. material 3). Specimens have been collected using pyrethrin fog applied to trunks and logs, from leaf litter, and also from flood debris.

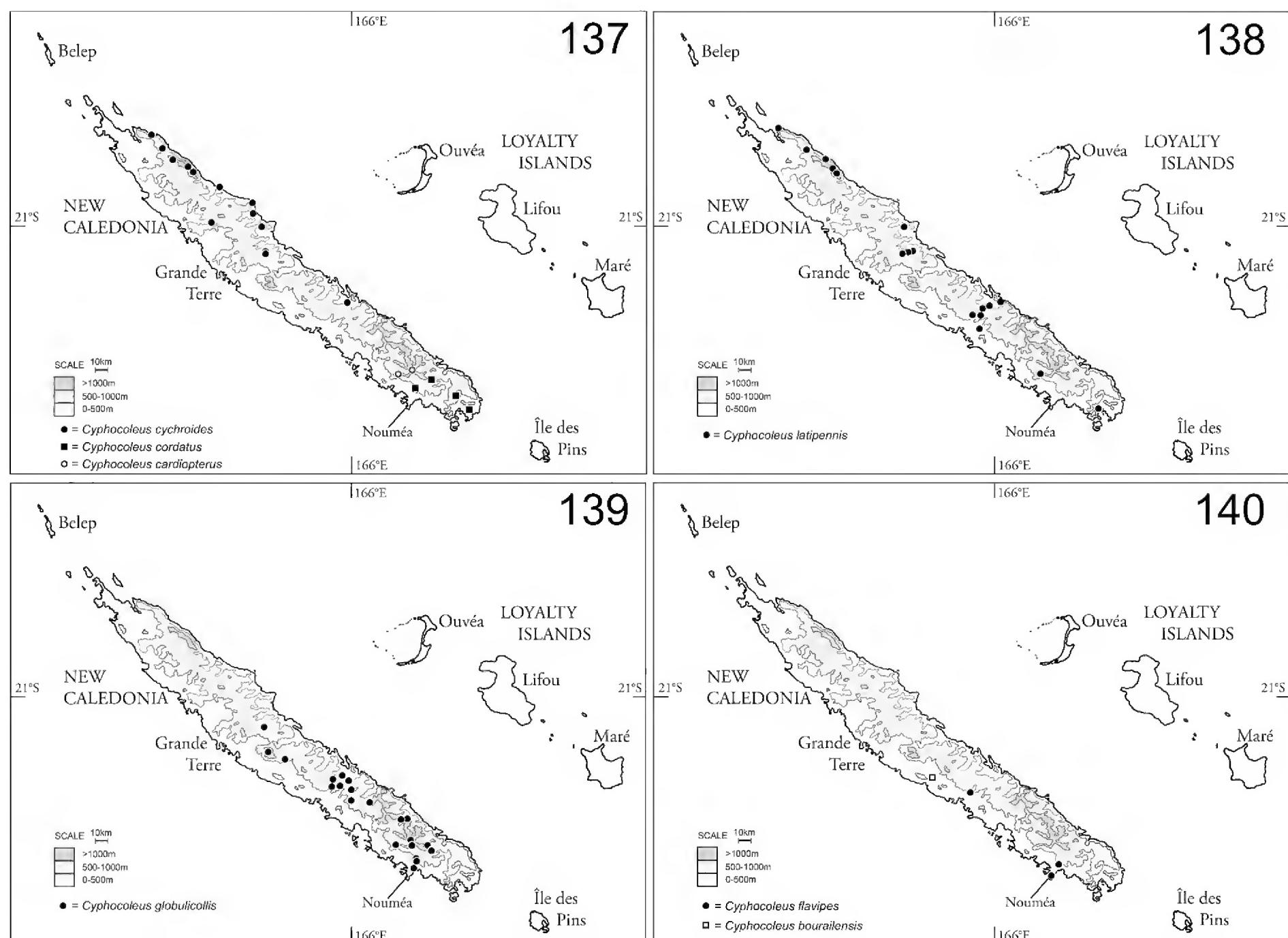
16. *Cyphocoleus cordatus* sp. n.

<http://zoobank.org/426B2B2A-6F48-4ABA-8601-EC74A69FB77E>

Figures 31, 116, 123, 134–135, 137

Diagnosis. This species and its adelphotaxon *C. cardiopterus* (Figs 123, 124) are characterized by an orbicular pronotum with lateral and basal marginal beads continuous arcuate around the pronotal base. The pronotal disc is at most shallowly wrinkled, and is covered with well-developed microsculpture, a transverse mesh on median disc, and isodiametric mesh laterad the shallow parasagittal impressions. Both species also differ from all other *Cyphocoleus* in the presence of a deep lateral fovea near the front of the mesepisternum, immediately posterad the hind margin of the proepimeron. The elytral striae of *C. cordatus* are punctate, the punctures limited to the depths of the very deep striae, whereas in *C. cardiopterus* the punctures are larger; expanding strial breadth to apex of elytra. The two species can also be diagnosed by elytral microsculpture; in *C. cordatus* the elytra bear transverse-line microsculpture, whereas in *C. cardiopterus* the beetles exhibit elytra covered with an isodiametric mesh. Standardized body length 6.1–7.2 mm.

Description (n = 5). Head capsule relatively broad, little narrower than prothorax, genae slightly convex anterad distinct, moderately constricted neck; eyes distinctly convex, oriented toward upper surface of head, ocular ratio quite variable, 1.43–1.50, 16 ommatidia across horizontal diameter of eye; frons with paired, rugose depressions that bracket median ridge, the ridge narrowed apically due to anterior broadening of depressions; frontal grooves broad, deep, expanded anterad to surround median frontal tubercle, their surfaces arcuately wrinkled; mandibles very elongate, length $2.6 \times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderate, scape length $2.5 \times$ maximal breadth; gena setose, subgenal seta present. Pronotum with front angles angulate, anterior pronotal margin broadly concave; median base continuously margined, bead elevated across base well above scutellum; median longitudinal impression deep, finely incised at depth, straight, extended basally to deep transverse groove just inside basal marginal bead, extended anteriorly nearly to well-defined anterior marginal collar that extends to front angles; anterior transverse impression by deep



Figures 137–140. Distribution maps of *Cyphocoleus* spp.: 137, *C. cychroides*, *C. cordatus*, *C. cardiopterus*; 138, *C. latipennis*; 139, *C. globulicollis*; 140 *C. flavipes*, *C. bourailensis*.

groove defining anterior limit of shallow transverse wrinkles, anterior callosity smooth, slightly convex behind anterior marginal collar; proepisternum extended beyond marginal bead, visible in dorsal view; proepisternum mostly smooth, with irregularities associated with shallow isodiametric microsculpture; prosternal process deeply, narrowly depressed medially before procoxae, narrowly medially depressed ventrally, posterior face with expanded triangular surface ventrally, median ridge invaginated dorsally. Elytra broadly cordate, basal margin sinuously recurved laterad depressed parascutellar striole, basal groove with deep pit at base of fourth stria; humerus broadly extended laterally at bases of striae 5–8, then evenly curved posterad outside anterior series of lateral elytral setae; discal intervals broadly convex, striae deep, all intervals of subequal convexity; parascutellar seta present, situated twice as far from basal margin than from suture, articulatory socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as (5)6 + (1) + (7)8, the articulatory sockets papillate; both subapical and apical elytral setae present, their articulatory sockets subequal; subapical sinuation shallowly concave, lateral portion of concavity joined to depressed lateral margin in broad curve, medial portion near suture nearly straight; elytral apices conjoined or nearly so, no or little invagination of apical margin at fused suture. Metepisternal dorsal length $0.9 \times$ diagonal width; metasternum with deep, circular median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.24; mt4 length to apex of outer lobe $1.6 \times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture on vertex dense transverse mesh; pelage little developed, head capsule, pronotum, and elytra with sparse distribution of exceedingly short microsetae, visible only in lateral view; pro-, meso-, and metasternites, and mediobasal portions of visible abdominal ventrites 2 and 3 with exceedingly short setae, other ventrites and legs glabrous except for macrosetae. Coloration of head capsule and prothorax piceous; elytra dark rufous with silvery iridescent reflection due to microsculpture; pterothoracic ventrites and elytral epipleura rufopiceous, abdominal ventrites rufous; femora dark rufous with piceous cast; tibiae rufobrunneous; tarsi rufoflavous.

Male genitalia (n = 4). Male aedeagal median lobe robust, broadly parallel sided over basal 3/4 of length, dorsoventral breadth at midlength $0.33 \times$ distance from tip to

base of closed basal bulb (Figs 134, 135); lobe apex only briefly extended beyond ostial opening, tip rounded (Fig. 134) to sub acuminate (Fig. 135); internal sac with large, heavily sclerotized, obtuse ventral tooth, the tooth surrounded by short, heavily sclerotized microtrichia (Fig. 135); sac length $2 \times$ breadth.

Female reproductive tract (n = 1). Bursa copulatrix vase-like, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite 2.75 maximum breadth (dissection compressed under cover slip) (as in Fig. 109); bursal walls thin, translucent, luminal surface with thick band of long thick setae surrounding midlength; basal gonocoxite with apical fringe of four to five setae (Fig. 116); apical gonocoxite narrowly subtriangular with narrowly rounded apex and two lateral ensiform setae.

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA 11822 / 22°19'Sx166°55'E 480 m / Foret Nord site 1.rainfor. / 2–3 Dec 2004 pyrethrum / CJ Burwell & GB Monteith // QUEENSLAND / MUSEUM LOAN / Date: July 2005. No. LE 05.24 [green label // HOLOTYPE / *Cyphocoleus* / *cordatus* / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (18 specimens). NEW CALEDONIA: Rivière Bleue, Haute Pourina, 800 m el., pyrethrum trees & logs, 22°06'S, 166°38'E, 22-xi-2000, Monteith (QMB, 4; lot no. 11210), Pourina track, 900 m el., pyrethrum trees & logs, 18-xi-2001, Monteith (QMB, 1; lot no. 8735), L'Houp Geant Trail, 330 m el., litter, rooting, 22°09.5'S, 166°30.8'E 13-iii-2007, Will (EMEC, 1), pyrethrum spray mossy log, 22°09'S, 166°41.2'E, 13-iii-2007, Will (EMEC, 2); Mt. Koghi, 600 m el., leaf litter, 22°10.7'S, 166°30.4'E, 12-iii-2007, Will (EMEC, 1), montane forest, 22°10'S, 166°31'E, 22–24-v-1987, Platnick & Raven (AMNH, 2), 500 m el., pyrethrum trunks & logs, 22°11'S, 166°31'E, 22-xi-2000, Monteith (QMB, 1; lot no. 9931); Forêt Nord, site 1, rainforest, 480 m el., pyrethrum, 22°19'S, 166°55'E, 02–03-xii-2004, Burwell & Monteith (QMB, 5; lot no. 11822).

Etymology. The species epithet *cordatus* – the Latin adjective heart-shaped (Brown 1956) – signifies the cor- date elytral shape characterizing both this species and its adelphotaxon, *C. cardiopterus* (Figs 123, 124).

Distribution and habitat. This species is restricted to the southern portion of Grande Terre, allopatrically south of the distribution of its adelphotaxon, *C. cardiopterus* (Fig. 137). Beetles have been collected via pyrethrin spray of mossy logs and tree trunks, as well as within leaf litter.

17. *Cyphocoleus cardiopterus* Chaudoir, 1877

Figures 109, 124, 136, 137

Diagnosis. The diagnosis of *C. cordatus* should be consulted to determine the characters that uniquely circumscribe this species and its adelphotaxon (Fig. 46). *C. cardiopterus* (Fig. 124) can be diagnosed from its sister species (Fig. 123) by the presence of distinctly punctate

elytral striae, the punctures expanding striae breadth to apex of elytra. The two species can also be diagnosed by elytral microsculpture; isodiametric in this species versus transverse-line microsculpture in *C. cordatus*. Standardized body length 6.5–7.2 mm.

Description (n = 5). (The description of *C. cordatus* can serve for this species, with the following exceptions to accompany the diagnostic characters presented above). Lateral elytral setae arranged as 6 + (1) + 7(8), articulatory sockets slightly upraised above cuticular surface, not papillate; elytral disc rufopiceous, without iridescent reflection.

Male genitalia (n = 1). Male aedeagal median lobe robust, broadly parallel sided over basal 2/3 of length, dorsoventral breadth at midlength 0.3 \times distance from tip to base of closed basal bulb (Fig. 136); lobe apex only briefly extended beyond ostial opening, tip rounded; internal sac with broadly angled though lightly sclerotized area on ventral surface, the remaining sac surface with lightly sclerotized, very short microtrichia; sac length 2 \times breadth. The broad, lightly sclerotized region on the ventral sac surface corresponds in position to the heavy sclerotized sac tooth observed in males of *C. cordatus*, supporting the homology of these structures. That the structures are not identical is supported by the similar sclerotization of the median lobe, and by the different eye configurations (Figs 123, 124) that also diagnose these species.

Female reproductive tract (n = 1). Bursa copulatrix vase-like, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite 2.75 maximum breadth (dissection compressed under cover slip) (Fig. 109); bursal walls thin, translucent, luminal surface with thick band of long thick setae surrounding midlength; basal gonocoxite with apical fringe of four to five setae (as in Fig. 116); apical gonocoxite narrowly subtriangular with narrowly rounded apex and two lateral ensiform setae.

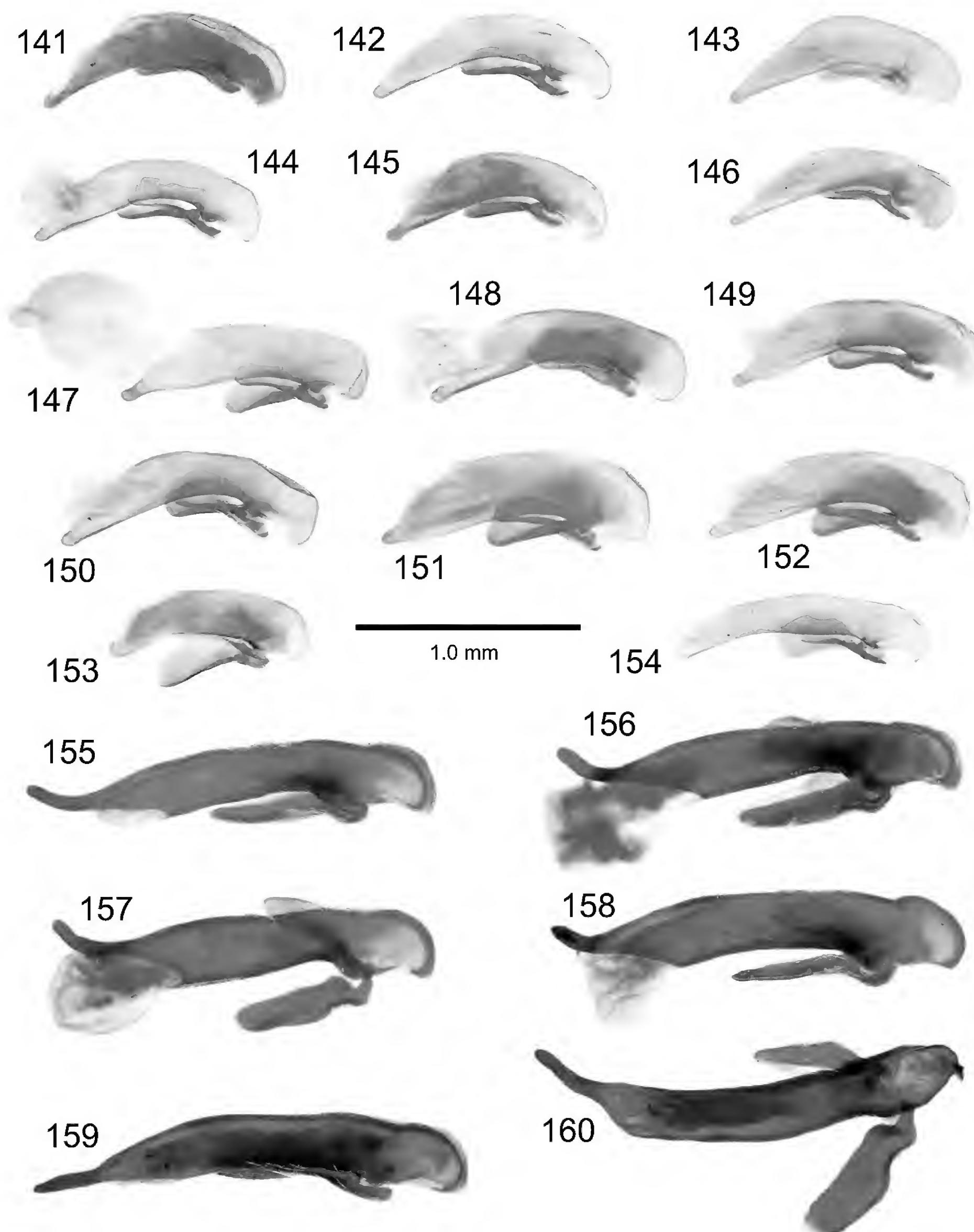
Type. Holotype female (MNHN): Ex Musæo / Chaudoir (red-inked white label with red border) // HOLOTYPE / *Cyphocoleus* / *cardiopterus* / Chaudoir 1877 (black-bordered red label). Holotype status is based on Chaudoir's (1877: 196) statement: "C'est également de M. Sallé que j'ai eu cet insecte." Mt. Mou hereby designated type locality.

Distribution and habitat. This species is known from Mt. Mou and near Mt. Dzumac, occupying a distribution allopatric and to the north of its adelphotaxon, *C. cordatus* (Fig. 137, Suppl. material 3).

18. *Cyphocoleus globulicollis* Fauvel, 1882

Figures 91–98, 110, 117, 125, 139, 141–152

Diagnosis (n = 5). Beetles comprising this species (Fig. 125) exhibit a pronotal disc with distinct transverse wrinkles bordered laterally by deep parasagittal impressions, and a body surface covered with a well-developed pelage of evident, elongate microsetae. These setae are especially visible on the vertex and frons, even occurring between



Figures 141–160. Male aedeagal median lobe and associated parameres of *Cyphocoleus* spp., dextral view: 141–152, *C. globulicollis*; 141, Aoupinié; 142, Me Maoya; 143, Col de Roussettes; 144, internal sac partially everted, Gelima; 145, Col d'Amieu; 146, Mt. Do; 147, internal sac everted, Ningua; 148–150, Mt. Dzumac Rd; 151–152, Mt. Koghi; 153, *C. flavipes*, Yahoué; 154, *C. bourailensis*, Bourail; 155–158, *C. subulatus*; 155, La Crouen; 156, Mt. Rembai; 157, Col d'Amieu; 158, Mt. Koghi; 159–160, *C. iledespinsensis*, Île des Pins; 159, dextral view; 160, ventral view.

the ommatidia on the surface of the slightly convex eyes: each eye with 12–13 ommatidia across the horizontal diameter. The elytra are broadly ovoid, with intervals 3–7 very convex, subcarinate basally. The elytral surface is glossy, with only very shallow transverse sculpticells visible over portions of the surface. Standardized body length 4.8–6.7 mm.

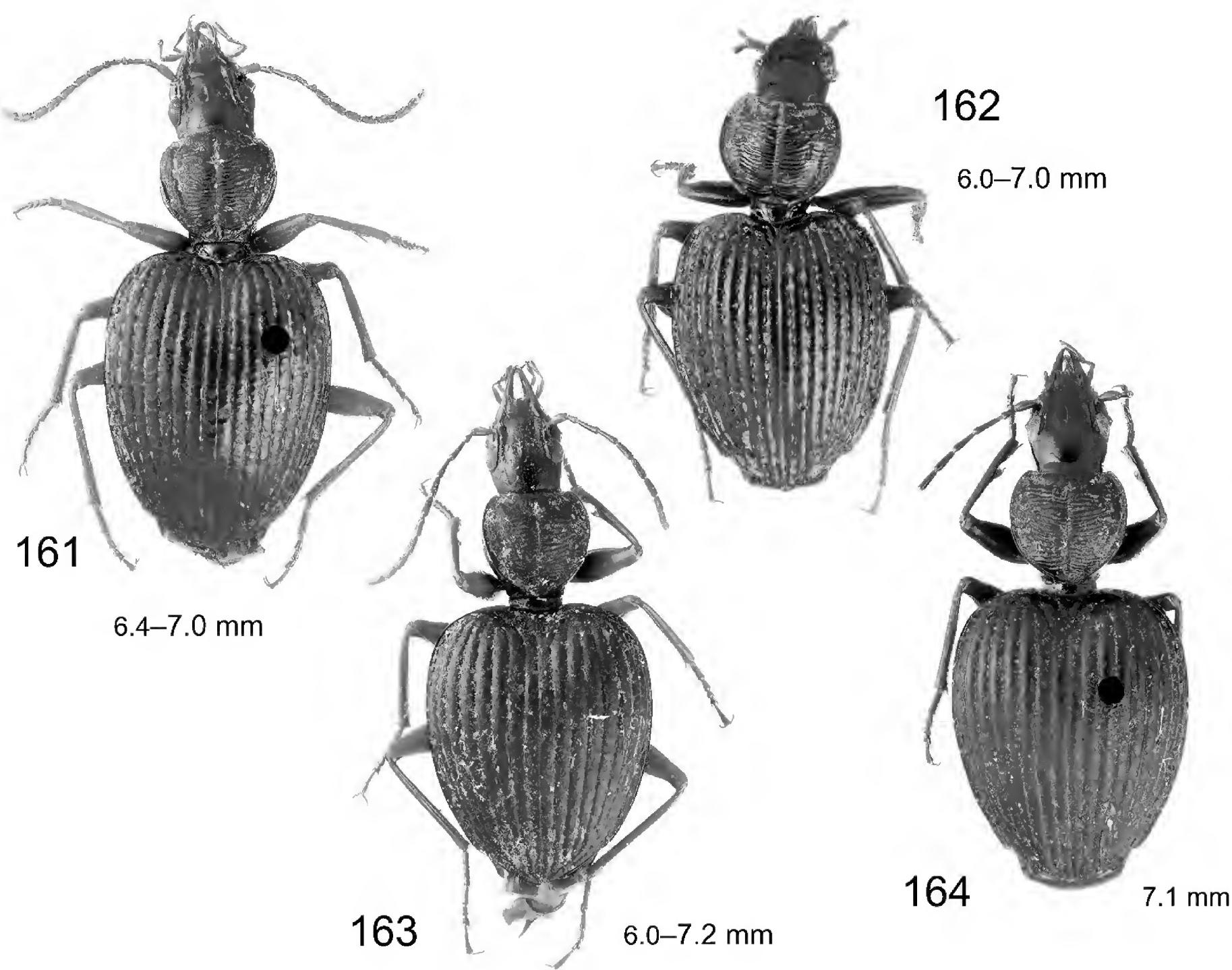
Description. Head capsule parallel-sided, appearing “reduviidoid”, the small, little-convex eyes only slightly extended beyond the genal profile in dorsal view; neck only slightly depressed medially, genae only indistinctly narrowed laterally before pronotal front angles; frons with narrow median longitudinal crest surrounded by flattened, rugose, lateral areas that lie mesad the deep, sinuous frontal grooves; frontoclypeal suture reduced, difficult to trace, frontal grooves apparently extended onto clypeus; mandibles elongate, length $2.1 \times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length $2.5 \times$ maximal breadth; gena setose, subgenal seta present. Pronotum with front angles protruded, angulate, the angle right to slightly acute; lateral marginal carinae extended to base, slightly sinuate just before depressed median base, the marginal bead across base irregularly interrupted by convex basal wrinkles of disc; median longitudinal impression deep and broad, separating discal wrinkles, extended nearly to anterior margin but deepest at juncture with transverse anterior impression; anterior transverse impression a depressed oblique border defining an irregularly surfaced anterior callosity bearing distinct longitudinal wrinkles; proepisternum bulging, distinctly extended beyond marginal bead in dorsal view; proepisternal surface dimpled, the irregularities mostly short vertical wrinkles near dorsal margin with proepipleuron, short longitudinal wrinkles ventrally; prosternum deeply depressed medially from pronotal anterior marginal bead to prosternal process, process broadly, slightly depressed on ventral face, posterior face with depressed ventral triangle and rounded medial ridge above. Elytra broadly ovoid, parascutellar region depressed and inflexed, basal margin sinuously subangulate basad stria 4, then broadly extended and posteriorly curved; sutural intervals elevated and fused into median callosity on middle of disc, intervals 3, 5, and 7, and to a lesser degree intervals 4 and 6, subcarinate, very convex on elevated basal portion of disc immediately posterad apex of parascutellar striole; striae deep, not visibly punctate except in extremely clean specimens where very small elongate punctulae can be seen in the deepest portion of the striae, these elongate depressions separated from each other by twice their length or more; parascutellar seta present, articulatory socket distinctly papillate, very upraised; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 6, the articulatory sockets distinctly papillate; both subapical and apical elytral seta present, the articulatory socket for apical seta much smaller, not papillate; subapical sinuation distinctly developed, lateral portion of concavi-

ty joined to depressed lateral margin in tightly rounded curve; elytral apices rounded, slightly separated by shallow invagination at fused suture. Mesepisternum impunctate; metepisternal dorsal length $1.1 \times$ diagonal width; metasternum with deep, circular median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.24; mt4 length to apex of outer lobe $2.0 \times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture on vertex densely transverse, shallow, difficult to trace on the glossy surface; higher areas between pronotal transverse wrinkles glossy, depressions of wrinkles and lateral flanges outside parasagittal groove covered with granulate isodiametric sculpticells, the surface matte; pelage well developed, head capsule, pronotum and elytra with densely distributed, evident microsetae, the setae on each elytral interval arranged in two irregular, longitudinal rows; prosternum with elongate pelage setae, meso- and metasternum largely glabrous, and meso- and metacoxae, and abdominal ventrites 2–3 medially with very short microsetae. Coloration of body dorsum piceous; thoracic sternites and elytral epipleura piceous, abdominal ventrites dark rufous; femora and tibiae rufopiceous, their articulation rufoflavous, tarsi rufobrunneous.

Male genitalia (n = 21). Male aedeagal median lobe variably robust, from gracile (Figs 144, 136) to more robust (Figs 147, 151, 152), dorsoventral breadth at midlength ranging from $0.16\text{--}0.22 \times$ distance from tip to base of closed basal bulb (Figs 141–152); lobe apex little extended beyond ostial opening, rounded; internal sac membranous without melanized microtrichia, length $1.5 \times$ breadth (Fig. 147). The substantial variation in robustness of the aedeagi for males assigned to *C. globulicollis* is not associated with geography, as a male from Mt. Dzumac Rd. in the southern portion of the range (Fig. 150) varies little from the male from Aoupinié at the northern margin (Fig. 141). Also two males from Mt. Koghi vary substantially in robustness (Figs 151, 152). All of these specimens exhibit the glossy cuticle with well-developed pelage of microsetae characteristic of *C. globulicollis*.

Female reproductive tract (n = 3). Bursa copulatrix columnar, distance from base of r gonocoxites to spermathecal basal sclerite $3 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 110); bursal walls thin, translucent, luminal surface smooth except for thin band of very fine setae over part of surface at midlength; basal gonocoxite with apical fringe of five to six setae (Fig. 117); apical gonocoxite broadly triangular with pointed apex and two lateral ensiform setae.

Type. Lectotype female (IRSN) hereby designated: Ile des Pins [and] M^t. Mou (two separate white labels glued to larger pink label) Coll. R. I. Sc. N. B. / Nou-



Figures 161–164. Dorsal habitus photographs of *Cyphocoleus* spp., environmental patina removed: 161, *C. flavipes* Yahoué; 162, *C. bourailensis*, Bourail; 163, *C. subulatus*, Mt. Koghi; 124, *C. iledespinsensis*, Île des Pins.

velle Calédonie / ex. coll. Fauvel/ rec. Deplanche // type (pink label with black border) // Coll. et det. A. Fauvel / *Cyphocoleus* 1882 / *globulicollis* Fauv. // LECTOTYPE / *Cyphocoleus* / *globulicollis* / Fauvel 1882 (black-bordered red label).

Nomenclatural note. Fauvel (1882: 250) described this species listing specimens from Mt. Mou and Île des Pins. The lectotype specimen has two labels glued to the pink IRSN museum card (above), one specifying “Île des Pins,” the second “Mt. Mou.” As these two localities are impossible to reconcile geographically on a single specimen, and as numerous other specimens of this species are recorded from Mt. Mou and vicinity, Mt. Mou is designated type locality, with Île des Pins considered to represent an unverified locality for this species.

Distribution and habitat. This species is distributed in the southern two-thirds of Grande Terre, being known from Aoupinié on the north to Montagne des Sources on the south (Fig. 139, Suppl. material 3). Beetles have been found in leaf litter, and via the application of pyrethrin fog to trunks and logs. The well-developed pelage of microsetae is associated with a deep layer of environmental patina developing on these beetles.

19. *Cyphocoleus flavipes* Fauvel, 1882

Figures 111, 118, 140, 153, 161

Diagnosis. Like *C. globulicollis* (Fig. 125) in the transversely wrinkled pronotal disc with deep parasagittal impressions and head without supraorbital setae, but differing through: 1, the much reduced dorsal pelage, the microsetae on head, pronotum, and elytra exceedingly short, visible only in lateral view; and 2, elytral striae distinctly punctate, the punctures broadening striae and separated from each other by about their own diameter (Fig. 161). Microsculpture is also better developed in this species, with the vertex of head and the pronotal disc, including elevated portions between transverse wrinkles, covered with an evident transverse mesh. The elytral intervals bear evident isodiametric and slightly transversely stretched sculpticells arranged in an irregular, transverse pattern. Standardized body length 6.4–7.0 mm.

Description ($n = 5$). Head capsule broad, genae short, neck only slightly constricted; eyes moderately convex but profile not exceeding curvature of gena on posterior portion of eye, ocular ratio 1.47–1.56, 15–16 ommatidia across horizontal diameter of eye; frons with well-de-

veloped median carina that is surrounded by transversely wrinkled median spot; frontal grooves narrow between eyes, sinuously extended anterad to a deep, rounded depression just posterad frontoclypeal suture; mandibles elongate, length $2.2 \times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length $2.75 \times$ maximal breadth; gena setose, subgenal seta present. Pronotum with front angles rounded, only slightly protruded, very obtuse; lateral marginal bead distinctly sinuate before depressed median base that is margined medially by an irregularly depressed bead continuous with the base of the median longitudinal impression; median longitudinal impression deep, broad, extended nearly to anterior marginal bead, with pit-like depression near juncture with anterior transverse impression; anterior transverse impression a shallow, irregular border on the anterior margin of the discal transverse wrinkles, defining a rugose, longitudinally wrinkled anterior callosity; proepisternum bulging, extended beyond marginal bead, visible in dorsal view, smooth; prosternal process convex anterad procoxae, slightly depressed medially on ventral face, broadly convex posteriorly. Elytra broadly cordate, basal margin slightly concave to base of fourth stria, then posteriorly curved across broad humeri; discal intervals moderately convex, all intervals of subequal convexity; elytral striae broad, deep, punctate, the punctures expanding striae breadth to elytral apex; parasutellar seta present, articulatory socket broadly papillate; dorsal elytral setae absent; lateral elytral setae arranged as $6 + 7$, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller, not papillate; subapical sinuation distinctly concave, lateral portion of concavity joined to depressed lateral margin in tightly rounded curve; elytral apices conjoined, margin not invaginated at fused suture. Mesepisternum impunctate; metepisternal dorsal length subequal to diagonal width; metasternum with broad, shallow median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two seta each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.23; mt4 length to apex of outer lobe $1.9 \times$ median tarsomere length, 3–4 ventrolateral setae each side. Pelage little developed, thoracic sternites with only a few very short microsetae, and abdominal ventrites and legs apparently glabrous except for macrosetae. Coloration of body dorsum piceous; prosternum piceous; meso- and metathoracic sternites and pleurites rufopiceous; abdominal ventrites rufous with piceous cast, apical margin of apical ventrite paler, brunneous to flavous; femora dark rufous basally and apically, but with flavous band just beyond midlength; tibiae rufous, matching femoral apex; tarsi brunneous.

Male genitalia (n = 3). Male aedeagal median lobe very short, broad, longer left paramere extended more than half distance from lobe tip to base of closed basal bulb (Fig. 153); lobe apex broadly extended beyond ostial opening,

tip broadly rounded, breadth of apical extension $0.6 \times$ distance from tip to ostial opening; internal sac membranous without melanized microtrichia (uneverted view).

Female reproductive tract (n = 2). Bursa copulatrix columnar, distance from base of gonocoxites to spermathecal basal sclerite $3.5 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 111); bursal walls thin, translucent, luminal surface smooth except for thin band of very fine setae at midlength; basal gonocoxite with apical fringe of five to seven setae (Fig. 118); apical gonocoxite subtriangular with pointed apex and two lateral ensiform setae.

Type. Lectotype female (IRSN) hereby designated: Yahoué Août / feuille morts au pied / d'un arbre (white label glued to larger pink label) Coll. R. I. Sc. N. B. / Nouvelle Calédonie / rec. / Savés / ex. coll. Fauvel // type (pink label with black border) // Coll. et det. A. Fauvel / *Cyphocoleus* / *flavipes* n. sp. / R. I. Sc. N. B. 17.479 // LECTOTYPE / *Cyphocoleus* / *flavipes* / Fauvel 1882 (black-bordered red label).

Distribution and habitat. This species is known only from the disjunct localities of Fonwhary in the northern portion of Province Sud, and Yahoué and Nouméa in the south of New Caledonia (Fig. 140, Suppl. material 3). The lone historical collecting record with ecological information includes a beetle collected in dead leaves at the base of a tree.

20. *Cyphocoleus bourailensis* sp. n.

<http://zoobank.org/7C2143D4-CD0B-4045-A06A-B9419D8DB79A>
Figures 119, 140, 154, 162

Diagnosis. This species shares the well-developed dorsal microsculpture, transversely wrinkled pronotum, and punctate elytral striae with *C. flavipes* (Fig. 161). But in beetles of this species, the pronotal transverse wrinkles are continuous across the pronotum, continued from the parasagittal impressions to the marginal bead, and the elytral striae punctures are larger and more circular causing greater lateral expansion of the striae (Fig. 162). The legs are also darker overall, without the pale median band on the femora as observed in *C. flavipes*. Standardized body length 6.0–7.0 mm.

Description (n = 5). Head capsule broad, genae short, neck only slightly constricted; eyes moderately convex but profile not exceeding curvature of gena on posterior portion of eye, ocular ratio 1.44–1.61, 16 ommatidia across horizontal diameter of eye; frons with chevron-shaped median elevation surrounded by hemicircular depressions, the broad part of the chevron continued anteriorly as median flat area bordered by frontal grooves; frontal grooves narrow with lateral marginal carina to mesad eyes, sinuously extended anterad to a broad, rounded depression just posterad frontoclypeal suture; mandibles moderately elongate, length $1.9 \times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae of moderate proportions, scape length $2.4 \times$ maximal breadth;

gena setose, subgenal seta present. Pronotum with front angles rounded, only slightly protruded, very obtuse; lateral marginal bead slightly sinuate before depressed median base that is marginated medially; median longitudinal impression finely incised, interrupted in part by transverse wrinkles, extended nearly to anterior marginal bead; anterior transverse impression a shallow, irregular border on the anterior margin of the discal transverse wrinkles, defining an irregularly, longitudinally wrinkled anterior callosity; proepisternum not extended beyond marginal bead in dorsal view, anteriorly with irregularly, arcuately wrinkled from front to dorsal margin; prosternal process slightly concave anterad procoxae, broadly and deeply depressed medially on ventral face, broadly convex posteriorly. Elytra broadly cordate, basal margin concave from scutellum to third stria, then extended anteriorly across broadly rounded humerus; small pits at the base of the parascutellar and third stria; discal intervals moderately convex, all intervals of subequal convexity; elytral striae finely incised at depth, deep, distinctly punctate, the punctures greatly expanding striae breadth throughout their length; parascutellar seta present, articulatory socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller, not papillate; subapical sinuation distinctly concave laterally, subangularly meeting lateral margin, margin slightly convex medially in dorsal view; elytral apices conjoined, margin not or minutely invaginated at fused suture. Mesepisternum impunctate; metepisternal dorsal length subequal to diagonal width; metasternum with broad, shallow median depression at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.25; mt4 length to apex of outer lobe 1.8× median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture well developed on head, isodiametric sculpticells on median elevation, vertex and neck with more transverse sculpticells defining a regular mesh; elevated portions of pronotal disc with shallow transverse-mesh microsculpture, wrinkled lined with granulate isodiametric sculpticells; elytral intervals with mix of transverse mesh, sculpticell breadth 3× length, and transverse lines loosely joined into a mesh; pelage little developed, head apparently glabrous, prothoracic and elytral disc with extremely short microsetae visible only in lateral view. Coloration of body dorsum piceous; prosternum piceous; meso- and metathoracic sternites, and abdominal ventrites dark rufous, apical margin of apical ventrite paler, brunneous to flavous; femora and tibiae dark rufous to match abdomen, tarsi slightly paler, brunneous.

Male genitalia (n = 3). Male aedeagal median lobe gracile, parallel sided, dorsoventral breadth at midlength 0.18× distance from tip to base of closed basal bulb (Figs 154); lobe apex extended little beyond distal margin of

ostial opening, broadly rounded; internal sac membranous without melanized microtrichia (uneverted view).

Female reproductive tract (n = 1). Bursa copulatrix columnar, distance from base of gonocoxites to spermathecal basal sclerite at least 2× maximum breadth (dissection broken); bursal walls thin, translucent, luminal surface smooth in portion examined; basal gonocoxite with apical fringe of five setae (Fig. 119); apical gonocoxite broadly subtriangular with pointed apex and two lateral ensiform setae.

Types. Holotype female (MNHN): (dissected female, pointed with abdominal ventrites glued onto second point below) Bourail // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 // *Cyphocoleus* / n.sp. *latipennis* / female 1 Bourail / det. J.K. Liebherr 2015 // genitalia vial // HOLOTYPE / *Cyphocoleus* / *bouailensis* / J.K. Liebherr 2016 (black-margined red label).

Paratypes (7 specimens found in header-labeled series including holotype and labeled paratype; General Coleoptera Collection, MNHN): Bourail (dissected female remounted as holotype); 6 unlabeled (2 dissected males remounted on point and platen, 1 undissected male on original platen, 1 undissected male remounted on point (Fig. 162), 2 teneral specimens on original platens).

Etymology. The species epithet is based on the type locality Bourail, with the -ensis suffix denoting this locality.

Distribution and habitat. As this species is known only from a single series of specimens with the header specimens labeled Bourail, we know only the general collecting locality: Bourail (Fig. 140).

21. *Cyphocoleus subulatus* sp. n.

<http://zoobank.org/6839CC5D-ED40-4D10-BE41-1717E4A57D8E>

Figures 1, 26, 27, 32, 112, 120, 155–158, 163, 165

Diagnosis. Among species with orbicular pronotum and broadly cordate elytra, this species (Fig. 163) shares the possession of the posterior supraorbital seta with only *C. latipennis* (Fig. 122) and *C. iledespensis* (Fig. 164). Beetles of *C. subulatus* can be diagnosed from the former by presence of evident, transversely stretched isodiametric microsculpture on the head, not the shallow, difficult to trace transverse-line microsculpture of *C. latipennis*. Conversely, this species can be diagnosed from the latter by the pale antennae, and femora with flavous ground color and dark basal and apical bands, versus the uniformly fuscous antennae and femora observed in *C. iledespensis*. The eyes of this species are more convex, ocular ratio 1.54–1.57 compared to those of *C. iledespensis*, where the broad, little convex eyes result in a ratio of 1.49. If a male can be dissected, the differences in the aedeagal median lobes are distinctive (see male genitalia sections for the two species descriptions). Standardized body length 6.0–7.2 mm.

Description (n = 5). Head capsule ovoid, neck moderately constricted with genae moderately convergent behind eyes in dorsal view; eyes moderately convex, outer profile extended beyond curvature of gena behind eye,

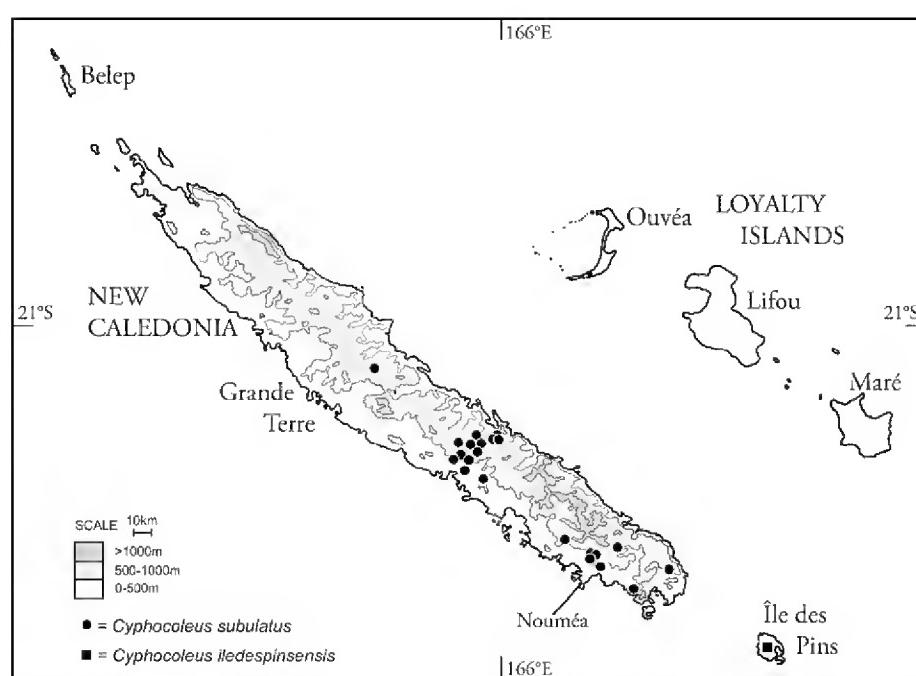


Figure 165. Distribution map of *Cyphocoleus subulatus* and *C. iledespensis*.

16–18 ommatidia across horizontal diameter of eye; frons with well-developed median carina that is surrounded by transversely wrinkled median flat spot; frontal grooves narrow, sinuous anteriorly from between eyes onto clypeus, frontoclypeal suture obsolete; mandibles moderately elongate, length $1.9 \times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length $2.5 \times$ maximal breadth; gena setose, subgenal seta present. Pronotum with front angles tightly rounded, slightly protruded, nearly right; lateral marginal bead distinctly sinuate before depressed median base that is margined medially by narrow bead; median longitudinal impression narrowly and finely incised, extended from just inside basal marginal bead nearly to anterior marginal bead, transverse wrinkles on either side of impression not aligned; anterior transverse impression very shallow, irregularly impressed in association with shallow longitudinal wrinkles on anterior callosity; proepisternum not visible in dorsal view, smooth ventrally, with fine vertical wrinkles along dorsal margin; prosternal process slightly convex medially anterad procoxae, with shallow medial depression ventrally, broadly convex posteriorly. Elytra broadly cordate, basal margin slightly concave to base of fourth stria, then posteriorly curved across broad humeri; discal intervals convex, intervals 3–5 slightly more convex, broader basally; elytral striae deep, narrow, impunctate; parascutellar seta present, articulatory socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller, not papillate; subapical sinuation distinctly concave, lateral portion of concavity joined to depressed lateral margin in broad curve, medial margin convex to suture; elytral apices conjoined, margin not or only slightly invaginated at fused suture. Mesepisternum impunctate; metepisternal dorsal length subequal to diagonal width; metasternum with broad, shallow median fossa at base of metepisternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females;

males with one seta each side of apical margin of apical ventrite, females with two seta each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.25; mt4 length to apex of outer lobe $1.6 \times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture well developed on pronotal disc, a combination of upraised isodiametric and transverse sculpticells, the surface matte; elytral microsculpture an irregularly present transverse mesh, sculpticell borders shallow, difficult to trace in glossier portions of surface; pelage little developed, head apparently glabrous, pronotal and elytral disc with sparsely distributed, extremely short microsetae, visible only in lateral view; prosternum with only a few very short microsetae, pterothoracic and abdominal ventrites and legs apparently glabrous except for macrosetae. Coloration of body dorsum and venter, including elytral epipleuron, uniformly piceous; legs paler, rufobrunneous with piceous cast except for flavous median femoral band (a minority of specimens lack this pale band and so have concolorous, rufobrunneous leg segments).

Male genitalia ($n = 7$). Male aedeagal median lobe elongate, heavily sclerotized, parallel sided from base to ostial opening; dorsoventral breadth at midlength $0.13 \times$ distance from tip to base of closed basal bulb (Figs 155–158); elongate lobe apex extended beyond ostial opening in a broad dorsally directed curve, tip tightly rounded, dorsoventral breadth at midlength of apical extension $0.18 \times$ distance from distal margin of ostial opening to tip; ostial opening on ventral surface of median lobe shaft (Fig. 157); sac covered with microtrichia, but without any heavily sclerotized structures, length at least $1.6 \times$ breadth.

Female reproductive tract ($n = 3$). Bursa copulatrix columnar, distance from base of gonocoxites to spermathecal basal sclerite $4 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 112); bursal walls thin, translucent, luminal surface smooth except for thin band of very fine setae at midlength; basal gonocoxite with apical fringe of five to six setae (Fig. 120); apical gonocoxite broadly subtriangular with pointed apex and two lateral ensiform setae.

Types. Holotype male (ANIC deposited in MNHN): NEW CALEDONIA / Col d'Amieu, 1800–2000 / 12–13 Dec., 1973 / G.B. & S. R. Monteith // HOLOTYPE / *Cyphocoleus* / *subulatus* / J.K. Liebherr 2016 (black-margined red label).

Paratypes (239 specimens). NEW CALEDONIA: Aoupinié, top camp, 850 m el., pyrethrum trees & logs, $21^{\circ}11'S$, $165^{\circ}18'E$, 02–03-xi-2001, Burwell & Monteith (QMB, 2; lot no. 8716); La Crouen, $21^{\circ}33'S$ $165^{\circ}55'E$, 16-iii-1961, Sedlacek (BPBM, 1); Col d'Amieu, 545–610 m el., $21^{\circ}33'S$, $165^{\circ}48'E$, 12–13-xii-1973, G. & S. Monteith (ANIC, 13), 18–19-xii-1973, G. & S. Monteith (ANIC, 2); Col d'Amieu, 6 km NNE, 300 m el., $21^{\circ}33.5'S$, $165^{\circ}51'E$, 13-xi-2000, Bouchard, Burwell & Monteith (QMB, 3; lot no. 9924; QMB, 2; lot no. 9923), pyrethrum trees & logs, 11-xi-2001, Burwell (QMB, 2; lot no. 8678), 390 m el., ex nr. *Mirasmius*, $21^{\circ}33.5'S$, $165^{\circ}45.6'E$, 16-iii-2007, Leschen (EMEC, 1; NZAC, 1); 440 m el., fogging logs,

21°33.5'S, 165°45.3'E, 16-iii-2007, Leschen (NZAC, 1); Mt. Kanala, 21°34'S, 165°56'E, 03-xi-1911, Sarasin & Roux (SMTD, 1); Ciu nr. Mt. Canala, rainforest, 21°34'S, 165°57'E, 01–03-i-1955 Wilson (MCZ, 2); Table Unio road, 500 m el., 21°34'S, 165°46'E, 14-xi-2000, Bouchard, Burwell & Monteith (QMB, 2; lot no. 9946), 800 m el., 21°34'S, 165°46'E, 14-xi-2000, Bouchard, Burwell & Monteith (QMB, 1; lot no. 9934); Canala, 4 km S Mia, 380 m el., 21°34.7'S, 165°58.3'E, river valley, rainforest, Wanat & Ruta (MNHW, 1); Mt. Rembai 650 m el., 21°35'S, 165°51'E, 09-v-1984 Monteith & Cook (QMB, 3), 700–900 m el., rainforest litter, 21°35'S, 165°51'E, 09-v-1984, Monteith & Cook (QMB, 9); Col d'Amieu Forest Station, 400 m el., 21°35'S, 165°50'E, 08–09-v-1984, Monteith & Cook (QMB, 4); Mt. Rembai top junction, 780 m el., hand collecting, rainforest, 21°35'S, 165°51'E, 30-xii-2004, Monteith (QMB, 1; lot no. 12007); Plateau de Dogny trail, 870 m el., litter, 21°37.2'S, 165°52.5'E, 15-iii-2007, Leschen & Will (EMEC, 1); Plateau de Dogny trail, 245 m el., flood debris, 21°37.8'S, 165°52'E, 15-iii-2007, Leschen (NZAC, 1), Will (EMEC, 12); Col d'Amieu litter, 21°37'S, 165°49'E, 06-ix-1990, Raven (QMB, 1); Farino, 5 km N, 400 m el., night collecting, 21°37'S, 165°46'E, 14-xi-2002, Burwell & Monteith (QMB, 2; lot no. 11186); Col d'Amieu, west slope, 470 m el., pyrethrum logs, 21°37'S, 165°49'E, 17-xi-2002, Monteith (QMB, 5; lot no. 11180), hand collecting, 21°37'S, 165°49'E, 25-xi-2003, Monteith (QMB, 1; lot no. 11426), pyrethrum trees & logs, 21°37'S, 165°49'E, 25-xi-2003, Monteith (QMB, 8; lot no. 11427), pyrethrum log w/ epiphytes, 21°37'S, 165°49'E, 27-i-2004, Monteith (QMB, 1; lot no. 11517), pyrethrum log w/o epiphytes, 21°37'S, 165°49'E, 27-xi-2004, Monteith (QMB, 14; lot no. 11516), pyrethrum trees & logs, 21°37'S, 165°49'E, 29-ix-2004 Monteith (QMB, 1; lot no. 11667); Saraméa, 2 km NE, 280 m el., 21°38'S, 165°52'E, 30-xi-2009, Schuh (NMHW, 2); Table Unio, 700–1000 m el., 21°43'S, 165°47'E, 10-v-1984, Monteith & Cook (QMB, 1); Saraméa, Plateau de Dogny, Bois mort, 21°46'S, 165°55'E, 23-vi-1971 (MNHN, 5); Mt. Mou, 380 m el., small stream, 22°04'S, 166°20'E, 23-xi-2009, Jäch (NMHW, 1); Col de la Pirogue, 22°05'S, 166°19'E, 23-i-1962, Krauss (BPBM, 2); Rivière Bleue, Kaori Geant, 22°06'S, 166°39'E, 11-xi-2000, Bouchard, Burwell & Monteith (QMB, 9; lot no. 9957), pyrethrum trunks & logs, 22°06'S, 166°39'E, 11-xi-2000, Monteith (QMB, 14; lot no. 9954), 160 m el., pyrethrum trees & logs, 22°06'S, 166°39'E, 19-xi-2002, Monteith (QMB, 2; lot no. 11202); 11–21-xi-2002, Monteith & Wright (QMB, 1; lot no. 11203), Pont Germain 160 m el., 22°06'S, 166°39'E, 11-xi-2000, Bouchard, Burwell & Monteith (QMB, 9; lot no. 9950), L'houp Geant Trail, 350 m el., 22°09'S, 166°41.2'E, 26-xi-2009, Jäch (NMHW, 1); Mt. Koghi, 22°10'S, 166°31'E, 26–30-i-1963, Kuschel (BPBM, 1), 480 m el., 24-x-2008, fogged log, Wanat (MNHW, 4), 500–800 m el., 23–27-x-1967, J. & M. Sedlacek (BPBM, 3), 500–750 m el., m, 25–26-x-1967, J. & M. Sedlacek (BPBM, 2), 610–670 m el., 20–23-xi-1973, G. & S. Monteith (ANIC, 8), 12–13-ii-1977, J. Balogh (RScC, 2), 500 m el., 26-viii-1978, S. & J. Peck (CNC, 2),

400 m el., 26-v-1984, Monteith & Cook (ANIC, 3), 400 m el., 26-v-1984, Monteith & Cook (ANIC, 2), rainforest 500 m el., sifted litter, 23-v-1987, Raven (QMB, 2), pyrethrum trunks & logs, 27-xi-2000, Monteith (QMB, 1; lot no. 9942), 750 m el., pyrethrum trunks & logs, 29-xi-2000, Monteith (QMB, 8; lot no. 9944); 500 m el., hand collecting, 27-i-2002, Monteith (QMB, 1; lot no. 8917), night collecting, 02–03-xi-2002, Burwell, Monteith & Wright (QMB, 2; lot no. 11088), 500 m el., 22-xi-2000, Bouchard, Burwell & Monteith (QMB, 2; lot no. 9932), dung pitfalls, 22-xi-2000, Monteith (QMB, 3; lot no. 9933), pyrethrum trunks & logs, 22-xi-2000, Monteith (QMB, 12; lot no. 9931), 700 m el., 22°10.5'S, 166°30.8'E, 12-iii-2007, Will (EMEC, 1), 550 m el., small streams, 22°10.5'S, 166°30.3'E, 25-xi-2009, Jäch (NMHW, 2), 485 m el., beating fungi & dead branches, 22°10.7'S, 166°30.4'E, 12-iii-2007, Leschen (EMEC, 2; NZAC, 1); Mt. Chapeau de Gendarme [= Mt. Malaoui], forest brook, under rocks, 22°11'S, 166°30'E, 22-x-1944, Herron (MSUC, 5), low pasture, 22-x-1944, Herron (MSUC, 1), under logs, 22-x-1944, Herron (MSUC, 1); Forêt de Thi to Hamma, 700–800 m el., 22°13'S, 166°32'E, 16-vii-1958, Malkin & Rageau (BPBM, 2); Forêt de Thi, 100–300 m el., 22°13'S, 166°32'E, 25-iii-1961, Sedlacek (BPBM, 2), 05-viii-1966, Oesterr. NC Exped. (RScC, 1), 30-x-1967, J. & M. Sedlacek (BPBM, 1), 100–300 m el., 07-ix-1979, Nishida (BPBM, 1), 150 m el., 21-v-1984, Monteith & Cook (ANIC, 2; QMB, 3); Pic du Grand Kaori, site 2, rainforest, 250 m el., hand collecting, 22°17'S, 166°53'E, 22–24-xi-2004, QMB Party (QMB, 2; lot no. 11772), pyrethrum, rainforest, 22–24-xi-2004, Monteith & Burwell (QMB, 1; lot no. 11773); Rivière des Pirogues Headwaters, 350–400 m el., 22°19'S, 166°44'E, 22-v-1984, Monteith & Cook (ANIC, 2; QMB, 4); Forêt Nord, site 2, rainforest, 200 m el., day hand collecting, 22°19'S, 166°55'E, 02–03-xii-2004, QMB Party (QMB, 3; lot no. 11829).

Etymology. The Latin adjectival *subulatus*, awl-shaped or pointed (Brown 1956), forms the basis this species' epithet based on the distinctively pointed male aedeagal median lobe (Figs 155–158).

Distribution and habitat. This species is known from the southern half of Grande Terre, with a northerly outlying locality, based on current specimens, at Aoupinié (Fig. 165). Beetles have been abundantly collected along the Saraméa-Canala Road, and also in the mountains outside Nouméa. Localities range in elevation from 100–900 m. Collecting situations are quite diverse, including dead branches with fungi, pyrethrin fogged logs with and without epiphytes, the margins of small streams, and within flood debris.

22. *Cyphocoleus iledespinsensis* sp. n.

<http://zoobank.org/FB56B4A9-0CB0-416E-8751-AC6DC4B08B11>
Figures 159–160, 164, 165

Diagnosis (n = 1). This species can be characterized as a dark, fuscous version of *C. subulatus*, its adelphotax-

on (Fig. 46). Only the less convex eyes (Fig. 164) – ocular ratio 1.49 – and the uniformly dark legs externally diagnose this species from its sister. The male genitalia can be referred to if a male is available for dissection. Standardized body length 7.1 mm. The two species are absolutely allopatric, with this species restricted to Île des Pins and *C. subulatus* distributed across the southern 2/3 of Grande Terre (Fig. 164).

Description. (The description of *C. subulatus* can serve for this species, with the following exceptions to accompany the diagnostic characters presented above). Head capsule narrowly ovoid, neck distinctly constricted with genae moderately convergent behind eyes in dorsal view; 17 ommatidia across horizontal diameter of eye; frons with narrow, elevated median carina that is surrounded by ovoid, transversely wrinkled median flat spot; frontal grooves narrow, sinuous anteriorly from between eyes onto clypeus, separated from supraocular groove by narrow ridge, frontoclypeal suture obsolete laterally, broadly and shallowly evident medially; mandibles moderately elongate, length $2.1 \times$ distance from antennal articulatory socket to anterolateral margin of labrum. Pronotum with front angles tightly rounded to angulate, slightly protruded, obtuse; median longitudinal impression narrowly and deeply incised; anterior transverse impression indicated laterally as oblique depressions extended toward front angles, absent medially where anterior wrinkle is extended anteriorly onto anterior callosity, very fine longitudinal irregularities traversing callosity. Elytral subapical sinuation distinctly concave, lateral portion of concavity joined to depressed lateral margin in tightly rounded curve; elytral apices rounded, narrowly separated by shallow invagination at fused suture, Abdomen with apical margin of apical ventrite shallowly concave medially in female, two setae each side of concavity. Microsculpture on elytral intervals much reduced, surface glossy, a transverse mesh or transverse lines present in depressed undulations of surface. Coloration of body dorsum and venter, including elytral epipleuron, uniformly piceous; legs rufopiceous.

Male genitalia ($n = 1$). Male aedeagal median lobe elongate, heavily sclerotized, parallel sided from base to ostial opening; dorsoventral breadth at midlength $0.13 \times$ distance from tip to base of closed basal bulb (Figs 159); elongate lobe apex porrect in dextral view (Fig. 159), curved to the right in ventral view (Fig. 160), dorsoventral breadth at midlength of apical extension $0.14 \times$ distance from distal margin of ostial opening to tip; ostial opening on left-ventral surface of median lobe shaft (Fig. 160).

Type. Holotype male (MNHN): (dissected, remounted on platen) // I. / des / Pins // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 // genitalia vial // HOLOTYPE / *Cyphocoleus* / iledespinsensis / J.K. Liebherr 2016 (black-bordered red label).

Etymology. The species epithet is based on the type locality Île des Pins; the -ensis suffix denoting this locality.

Distribution and habitat. The lone holotype is labeled only “I. des Pins” leaving the ecological situation and exact locality within which this species may occur

a mystery. To extrapolate from the known habitat of its sister species, *C. subulatus*, we can predict that beetles of this species occupy dead branches with fungi, rotten logs with and without epiphytes, and the margins of small streams.

Discussion

***Cyphocoleus* radiation.** The New Caledonian *Cyphocoleus* fauna exhibits substantial disparity in body forms. However when these forms are aligned using cladistic principles, the disparate body plans become explainable as the sequential evolution of salient characters, with these characters transforming the end products of the lineage in dramatic fashion. The groundplan for *Cyphocoleus* is built on a common ancestor who lacked flight wings, and thus evolved thickened cuticle and the robust body form as observed in *Cyphocoleus lissus* (Fig. 47). The eyes were small relative to the head, with the elongate head capsule not constricted into a neck. The elytra bore dorsal elytral setae in the third interval just as do most Carabidae. Also, the cuticular surface of the elytra bore very fine and short microsetae, these setae arranged in alternating rows down the lengths of the elytral intervals. In the groundplan these setae are so small as to be unapparent except with careful examination laterally across the cuticular surface.

The two successive branching lineages to come from the common ancestor – the clade of five species subtended by *C. heterogenus*, and *C. prolixus* (Fig. 46) – were transformed by the evolution of an elongate prothorax (Figs 48–50, 82–84). This prothoracic elongation is associated with narrowing of the pronotum, this narrowing resulting in distension of the proepisternum outside the dorsal profile of the notum. This tubularization of the prothorax is also a synapomorphy of all Odacanthina subordinate to *Lasiocera*. The head capsule is also constricted basally into a neck just before the juncture with the pronotum. These taxa also exhibited evolutionary increase in body size, with body lengths the largest in the radiation: 9.1–13.1 mm versus 6.7–8.2 mm for *C. lissus*. The bodies of these large beetles are also extremely narrow, with the legs greatly elongate. Thus these beetles are predicted to be exceedingly agile in their habitat, moving above the surface of mosses and other epiphytes on their long legs.

The sister group to the *C. prolixus* lineage (Fig. 46: A) adds several highly unique characters to the narrow, elongate body plan. It is at this point in the phylogeny of *Cyphocoleus* that the elongate pronotum evolves transverse wrinkles (Fig. 85). In *C. monteithi* we see the elytra transformed from narrow, little-convex sheaths to a globose, domed carapace that is substantially broader than the forebody (Fig. 85). It is also in *C. monteithi* and all subsequent descendant taxa that the varnish-like environmental patina is developed. In *C. monteithi* this patina consists of a surface varnish that can be flaked off using a minuten nadeln by the taxonomist interested in observing surface

microsculpture or punctuation of the elytral striae. In association with the evolution of this patina, the dorsal elytral setae are absent, though the parascutellar seta, the lateral series of elytral setae in the eighth interval, and the subapical and apical elytral setae remain. But these setae are situated at the top of papillate cuticular projections ensuring that the setal articulatory sockets are raised high above the surrounding elytral surface. Although it is as yet only informed conjecture, the strict phylogenetic association of environmental patina, dorsal setal loss, *and* papillate raising of articulatory sockets for those setae that remain suggests a selective interaction of varnish and setal evolution.

Subsequent to evolution of the environmental patina, the *Cyphocoleus* splits into two disparate clades. The first *C. miricollis* clade includes beetles that are smaller–body lengths 4.8–7.7 mm—but with significantly punctate striae on the elytra (Figs 99, 101–103). These punctate elytral striae are associated with very convex intervals, with carinae developing when odd intervals are more convex than even intervals (Fig. 101). These beetles also exhibit a greatly constricted neck resulting in a pedunculate head. The antennal scapes are broadened to achieve the profile of a cricket bat in *C. mirabilis*, *C. moorei*, and *C. lescheni*. The prothorax of the initially divergent extant taxon, *C. miricollis*, is similar to that of *C. monteithi* in dimensions, possession of deep transverse wrinkles, and prominent front angles (Figs 85, 99). These pronotal front angles, and hind angles as well, transform to prominent processes that may be flat and paddle-like (Fig. 101), or circular and expanded apically (Figs 102, 103) in the subsequently divergent species. It is also in these beetle species that the environmental patina is developed to its utmost condition, here as a means for complete crypsis as the body becomes covered with a dense, anastomosing mat of environmental debris. This debris appears to be wood fibres or fine bits of humus, and it is layered on the cuticle of the beetle's body within and to the height of a pelage comprising club-shaped setae. These setae are not positioned in the standard positions of carabid beetle macrosetae, but are an extreme development of pelage setae present in the *Cyphocoleus* groundplan. In the extreme case of *C. mirabilis*, *C. moorei*, and *C. lescheni*, the anastomosed layer of debris extends from the glossy body surface to a depth equal to the apices of the club-like setae and the anterior and posterior pronotal processes. Setal reduction beyond absence of the dorsal elytral setae also evolved in this clade: 1, all four species lack the apical elytral seta, though the subapical elytral seta remains; 2, *C. mirabilis*, *C. moorei*, and *C. lescheni* lack the parascutellar seta. That progressive thickening of the environmental patina was evolutionarily associated with progressive setal loss suggests that the presence of a very thick patina infused with environmental debris reduced the functionality of underlying setae, undercutting any selective advantage to their retention.

The adelphotaxon to the *C. miricollis* clade represents the final iteration of body form in *Cyphocoleus*, i.e. beetles with orbicular pronotum and broadly cordate elytra (Figs

104, 121–125, 161–164). As opposed to *C. miricollis* and associates, the head is not pedunculate, and the pronotum lacks prominent front angles. In *C. fasciatus* however, the pronotum exhibits prominent denticles at the hind angles, homologous (but only under fast character optimization) with the hind pronotal processes observed in *C. mirabilis* and allies. The pronotum of *C. fasciatus* and many taxa in this clade exhibit the usual median longitudinal impression, but also parasagittal impressions that longitudinally divide the surface of each side of the notum: e.g. *C. globulicollis* (Fig. 125). Although the elytral intervals are very convex on these beetles' cordate elytra, all intervals are of subequal development with the presence of elytral carinae. Also, the domed elytra appear completely fused into a carapace, as the elytral apices are tightly conjoined at the suture, without any apical emargination (Fig. 1). This would suggest that the elytra serve to maintain body integrity as the beetle moves between parallel surfaces: e.g. in the subcortical zone of decaying woody plants, between layers of terrestrial humus or debris, or within loose soil.

At 8.1–8.9 mm body length, *Cyphocoleus fasciatus* is the largest-bodied taxon in this clade, evolutionarily retaining a larger body size similar to that of *C. monteithi* (8.5–10.5 mm). All subsequently evolved taxa in the orbicular pronotum + cordate elytra clade measure 4.8–7.5 mm body length, with body sizes among all of the species broadly overlapping. Beetles representing this body form have been collected from a broad variety of ecological situations. This is especially so for the abundantly collected *C. subulatus*, where individuals have been found associated with dead wood, fungi, epiphytes, and stream margins with associated flood debris. Thus this body form is associated not only with the greatest number of known species, but also with the largest variety of microhabitats.

Environmental Patina Function. The development of a varnish-like patina that obscures the deeper features of the cuticle, such as pronotal transverse wrinkles and elytral striae, evolved once within *Cyphocoleus* in the common ancestor of *C. monteithi* and its adelphotaxon (Fig. 46). In its simplest state, the patina covers the cuticular surface, however environmental debris is not trapped within it, at least for the specimens studied for this revision. Beetles exhibiting this type of patina possess pelage setae over the body surface that are short and fine, the setae acuminate apically. In *C. fasciatus*, with longer pelage setae that are acuminate apically, the patina may be much thicker, incorporating environmental material: presumably fine plant fibres or particles of humus. The ultimately developed patina incorporating a thick layer of environmental debris is observed on beetles with elongate club-shaped setae: i.e. *C. mirabilis* and adelphotaxon (Fig. 46). Conversely, in species that exhibit a thin varnish-like patina without debris—e.g., *C. flavipes* and adelphotaxon (Fig. 46)—the dorsal pelage setae are much shorter, often unapparent except under high magnification. Nonetheless, presence of the pelage does not inevitably lead to patina development. The

ventral surfaces of beetles that exhibit dorsal pelage setae long enough to be associated with a debris-infused dorsal patina, exhibit setose ventral surfaces clean of debris. These ventral surfaces with pelage setae are predominantly the thoracic sternites, the metacoxae, and in some species the medial portions of the abdominal ventrites. Why these setose ventral surfaces remain clean of debris is unknown. Must some cuticular wax or other hydrocarbon be present to allow debris to adhere between the pelage setae? Do the beetles groom the ventral surfaces differently to maintain clean surfaces where the legs articulate? Does the manner of beetle locomotion promote development of patina materials on the dorsal surfaces? Regardless of how the patina is emplaced on the dorsal surfaces, its restricted presence there strongly suggests a primary role in crypsis.

Cenozoic History of New Caledonia. There is little controversy whether New Caledonia is associated with the Lord Howe Rise, and that this region of eastern Gondwana progressively rifted from the eastern margin of Australia from Late Cretaceous to Paleocene, 90–61 Ma (McLoughlin 2001, Schellart et al. 2006, Ladiges and Cantrill 2007). However the initial subduction of the Pacific Plate under the margin of Australia at 90 Ma was followed by accelerated Pacific Plate subduction that caused 1200 km of eastward movement of the subduction zone and crustal extension of the Lord Howe Rise (Schellart et al. 2006, fig. 3). This crustal extension resulted in the opening of several backarc basins and subsidence of various crustal blocks including New Caledonia. This geological scenario has been alternately interpreted to allow the continuous existence of subaerial lands coincident or near New Caledonia since Late Cretaceous (Ladiges and Cantrill 2007), or to disallow such subaerial lands until the Eocene, when it is hypothesized that New Caledonia or volcanic islands near it once again became subaerial (Schellart et al. 2006, Grandcolas et al. 2008). Thus there are starkly alternative histories hypothesized for New Caledonia that are relevant for any biogeographic analysis based on endemic New Caledonian taxa: 1, New Caledonia or an area close to it has persisted subaerially since the Late Cretaceous; or 2, New Caledonia includes Cretaceous formations however they are irrelevant for biogeographic analysis because the main island, Grand Terre, was submerged prior to 37 Ma.

The biogeographic pattern exhibited by Homethina is consistent with amphantarctic vicariance of Gondwana. Initial isolation of the Australian and South American mammal faunas is hypothesized to have started 64 Ma, with vicariance completed by 50 Ma (Woodburne and Case 1996); marsupials thus exhibiting a Gondwanan vicariant biogeographic pattern (Sanmartín and Ronquist 2004). Geological isolation of Australia and South America formerly adjoining Antarctica was fully achieved 35–30 Ma through nearly coincident opening of the Australo-Antarctic Gulf and Drake Passage (McLoughlin 2001, Lawver and Gahagan 2003, Livermore et al. 2005). Thus the age of the common ancestor of

Homethes + *Aeolodermus* and ((*Quammenis* + *Stenochela*) + *Diplacanthogaster*) is constrained to be no younger than 30–35 Ma (Fig. 166). Given that *Cyphocoleus* is the sister group to these five genera, the common ancestor of Homethina must be dated to before 30–35 Ma as well. Ober and Heider (2010) estimated the age of the common ancestor of tribes Peleciini and Odacanthini to be 100–105 Ma using the r8s method and sequence data from 28s rDNA plus the wingless gene. Their taxon sampling of Odacanthini included species of *Actenonyx*, *Pentagonica*, *Scopodes*, plus species in six genera of Odacanthina: three of the four odacanthine subtribes recognized here. They estimated the time of divergence of Pentagonalina and Odacanthina at 65 Ma. Integrating the currently proposed subtribal relationships (Figs 45, 46) with a date of origin of 100 Ma for the tribe and 65 Ma for the ancestor of Pentagonalina + Odacanthina supports the origin of Homethina between the time of origin of the tribe, 100 Ma, and the divergence of Pentagonalina and Odacanthina, 65 Ma. Thus under this interpretation, the diversification of the Cretaceous-aged Odacanthini was temporally concordant with Gondwanan vicariance, and therefore occupation of New Caledonia by *Cyphocoleus* supports Grand Terre's consistent presence as a subaerial entity throughout the Cenozoic. This interpretation also supports the occupation of a consistently subaerial New Zealand by *Actenonyx* over that same Era, as *Actenonyx* would have been present on New Zealand long before the Oligocene drowning event proposed for 34–23 Ma (Campbell and Hutching 2007).

What if we were to accept the geological scenario whereby New Caledonia subsided completely during crustal extension of the Australian Plate, and only re-emerged 37 Ma? This could be rectified with the molecular dating estimates by hypothesizing the extinction of lineages related to *Cyphocoleus*, these extinct lineages “marking time” at “an undisclosed location” during the interval between the Cretaceous origin of Odacanthini and an Eocene reemergence of New Caledonia (Fig. 166, dashed line denoting post-submergence dispersal). By this reasoning *Cyphocoleus* could represent a revenant clade (Sharma and Wheeler 2013); i.e. a clade that experienced a substantial extinction bottleneck and radiated recently. Based on Sharma and Wheeler's (2013) criteria, however, *Cyphocoleus* does not present the attributes of a revenant clade, as it is a speciose and anatomically disparate radiation, and many of the taxa are known only from single localities (Figs 77, 79, 80, 81, 140, 165). Nonetheless, if one assumes post-emergence colonization over water from Australia less than 37 Ma as the basis for the New Caledonian *Cyphocoleus* radiation, it would require the window of opportunity for dispersal to last only 2–5 Ma, being constricted at an upper bound by amphantarctic vicariance across the Australo-Antarctic Gulf, 35–32 Ma. Given the phylogeny of Odacanthini, a similar temporal eclipse and subsequent dispersal event must also be implicated as the basis for the New Zealand endemic *Actenonyx*. In this instance,

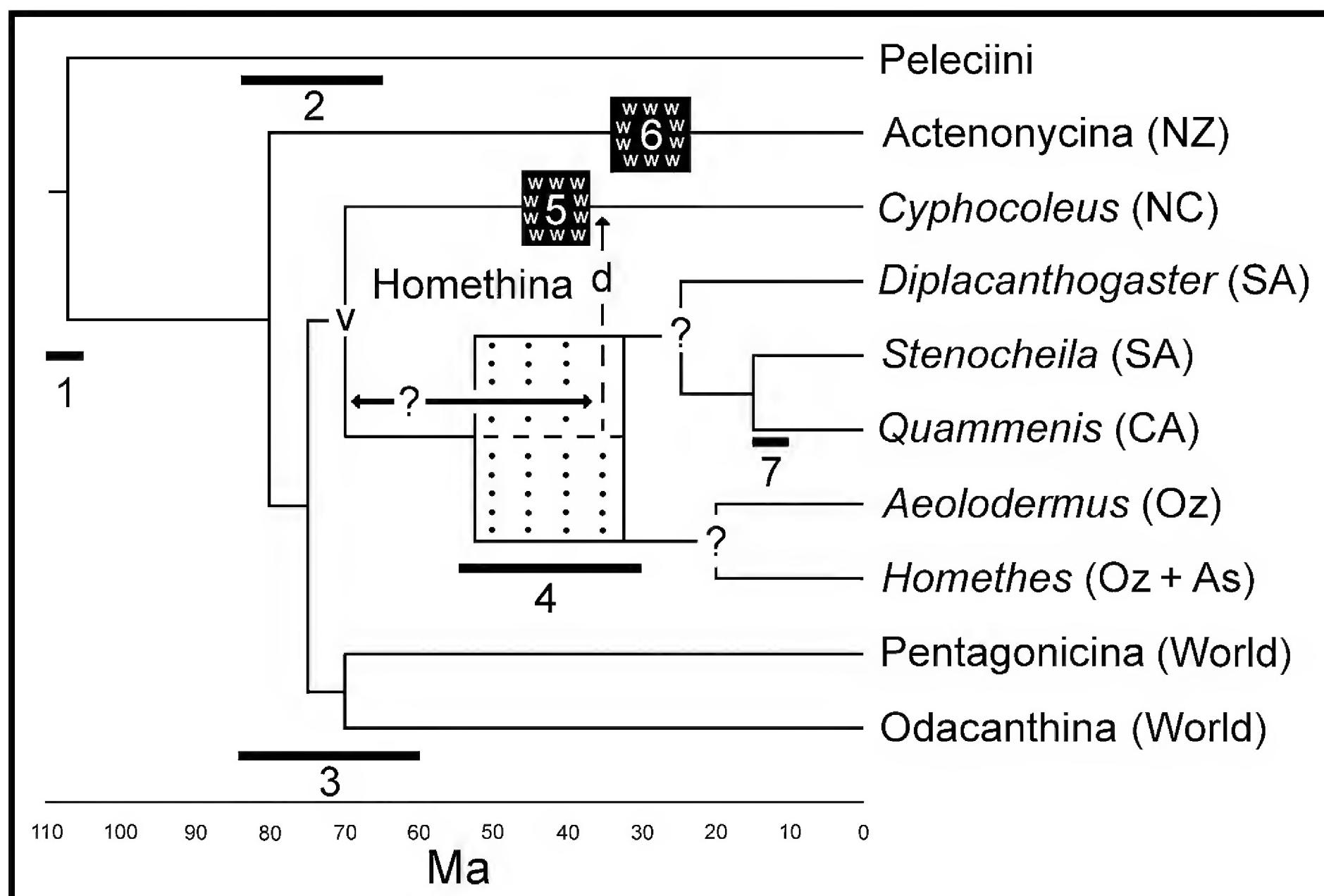


Figure 166. Diversification history of odacanthine subtribes and generic-level taxa within Homethina placed in temporal context defined by major geological events and molecular dating estimates (Ober and Heider 2010). Major events and dating estimates constraining historical relationships of the represented taxa include: 1, 100–105 Ma, estimated age of origin of Odacanthini relative to its proposed adelphotaxon Peleciini (Ober and Maddison 2008, Ober and Heider 2010); 2, 84–65 Ma, estimated divergence times of lineages within Odacanthini, represented in this study by Actenonyicina, Pentagonicina, and Odacanthina (Ober and Heider 2010); 3, 84–61 Ma, rifting of Zealandia, including New Caledonia and New Zealand, from Australia (McLoughlin 2001, Ladiges and Cantrill 2007); 4, 50–30 Ma, extended rifting and increased isolation of Australia and South America from Antarctica due to opening of the Tasman Sea at 50 Ma (Woodburne and Case 1996, Sanmartín and Ronquist 2004), development of the Australo-Antarctic Gulf at 35–32 Ma (McLoughlin 2001, Lawver and Gahagan 2003), and opening of Drake Passage at 34–30 Ma (Livermore et al. 2005); 5, 46–37 Ma, hypothesized submergence of New Caledonia (Grandcolas et al. 2008); 6, 34–23 Ma, hypothesized Oligocene drowning of New Zealand (Campbell and Hutching 2007); 7, 15–10 Ma, closing of Panamanian Isthmus establishing subaerial contact between South and Central America (Montes et al. 2015). Time of divergence of *Cyphocoleus* unconstrained due to lack of molecular-dating data. Under vicariance hypothesis (v), the ancestor of *Cyphocoleus* was emplaced on Zealandia in Late Cretaceous (event 3). Under dispersal scenario (d with dashed line), *Cyphocoleus* dispersal to New Caledonia is constrained at the lower bound by reemergence of Grande Terre after putative Oligocene submergence (event 5), and at upper bound by amphantarctic vicariance at Austral-Antarctic Gulf that isolated Antarctica from Australia (event 4).

one would have to find a land mass that the New Zealand precintive *Actenonyx* could occupy until after the proposed 34–23 Ma Oligocene drowning of New Zealand (Campbell and Hutching 2007), as the common ancestor of the Australian and South American Homethina certainly evolved more than 30 Ma, and *Actenonyx* is hypothesized to have evolved long before that as the product of the first Cretaceous-aged divergence event within Odacanthini. Having ancestors of both *Actenonyx* and *Cyphocoleus* colonize their respective present-day microcontinental ranges during different spans long after the Cretaceous origin of the tribe Odacanthini beggars credibility. Nevertheless, arguing from the various attri-

butes of the extant New Caledonian *Cyphocoleus* radiation—flightlessness, morphological disparity, geographic endemism—may not satisfy all biogeographers regarding the contribution of *Cyphocoleus* to knowledge of New Caledonia’s Cenozoic biogeographic history. Yet based on this revision, and the attendant phylogenetic context proposed for *Cyphocoleus*, two very explicit, alternative biogeographic explanations become available. The more general and less assumption-laden vicariance-based hypothesis is preferable under a logical parsimony framework. Additional investigation of the date of the origin for the *Cyphocoleus* radiation will test this currently preferred general hypothesis.

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Supplementary material 1**Checklist of taxa represented in cladistic analysis of Odacanthini**

Authors: James K. Liebherr

Data type: Taxonomic checklist

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Supplementary material 2**NONA format data file for cladistic analysis of Odacanthini**

Authors: James K. Liebherr

Data type: Phylogenetic analysis data file

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Supplementary material 3**Specimen records for previously described *Cyphocoleus* spp.**

Authors: James K. Liebherr

Data type: Species distributions and specimen repositories

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Spotted males, uniform females and the lowest chromosome number in Tettigoniids recorded: Review of the genus *Gonatoxia* Karsch (Orthoptera, Phaneropterinae)

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Abstract

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The genus *Gonatoxia* Karsch, which was synonymized with *Dapanera* Karsch by Massa (2015), is re-established. Data on habitat, biology, ecology, the acoustics and on chromosomes are provided as well as a key to the species. The male of *G. immaculata* Karsch and the female of *G. maculata* Karsch are described. *G. furcata* sp. n. from the Udzungwa Mountains of Tanzania and *G. helleri* sp. n. inhabiting coastal and lowland wet forest are newly described. All species have calling songs consisting of very short, resonant syllables, produced in species specific intervals, and with peak carrier frequencies between 13 and 24 kHz. In respect to chromosome numbers *Gonatoxia* species showed extreme differences (from 29 to 7) suggesting rapid evolutionary changes. *G. helleri* sp. n. so far is the tettigoniid species with the lowest number of chromosomes at present. *Gonatoxia* species may be used as bioindicators, their presence suggesting valuable habitats that are vanishing rapidly in East Africa.

Introduction

Lowland and coastal forests in East Africa are diminishing rapidly although their importance as hotspots of biodiversity and endemism are acknowledged (Burgess and Clarke 2000; Burgess et al. 2007). Coastal and lowland wet forests also harbor a high biodiversity of Orthoptera. Many Orthoptera species have a narrow ecological niche and are restricted to well defined plant assemblages (e.g. Hemp and Hemp 2003, Hemp 2005a, b) and can thus be used as bioindicators (Hemp et al. 2014), useful tools to

identify habitats deserving protection. The presence of e.g. *Tropidonotacris grandis* indicates dry deciduous forest or “Obstgartensteppe”, two habitat types highly endangered by habitat destruction in Tanzania (Hemp et al. 2014). The Phaneropterinae *Parapryrrhicia acutilobata* on the other hand indicates lowland wet forest, a forest type of which only few patches remained in East Africa (Hemp et al. 2016). If coastal forest is opened up or converted to grasslands the faunistic composition changes completely, mostly endemic and often flightless forest species are replaced by wide-spread and mainly fully mobile taxa (Hemp 2005b).

Until recently species of the genus *Gonatoxia* were poorly collected and little or no data were available on their biology, habitat or chromosomes. Karsch (1889) erected the genus *Gonatoxia* and described two species on two specimens, *G. immaculata* on a female from the Usambara Mountains, and *G. maculata* on a male from Somalia. In naming the species he referred to the maculae on the tegmina, present in the male of *G. maculata*, absent in the female *G. immaculata*. Very few specimens were collected of *G. maculata* since its description and stored in various entomological collections. For *G. maculata* a larger distribution area is suggested since the few known specimens were collected from Somalia, Kenya and Tanzania. For *G. immaculata* only the female holotype was known. When screening savanna habitats around Kilimanjaro at night larger numbers of *G. maculata* specimens could be collected in the past couple of years. When focusing on Tanzanian coastal and lowland wet forests specimens of *G. immaculata* were found. Only the study of a larger series of individuals clarified the status of the species which is now presented in this study. *G. furcata* sp. n. and *G. helleri* sp. n. are newly described and data on morphology, ecology, acoustics and chromosomes provided.

Material and methods

Measurements. The total body length refers to the body length of the insect without tegmina. In females the ovipositor is not included in the body length, its length is taken from the tip to the base of the subgenital plate not considering the curvature. Length of tegmina are taken from above.

Depositories. NHML: British Museum, Natural History, London, U.K. MfN: Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Germany. ZMUC: Zoological Museum, Copenhagen, Denmark.

Acoustics. Songs were recorded in the laboratory using a digital bat detector (Pettersson D1000X) with sampling rates between 100 and 192 kHz and, additionally, a Sony ECM-121 microphone (frequency response relatively flat up to 30 kHz; own tests) connected to a personal computer through an external soundcard (Transit USB, "M-Audio"; 64-kHz sampling rate).

Specimens recorded. *Gonatoxia helleri* sp. n./Hemp 2016: Tanzania, Udzungwa Mts., 6 males (3 collected in the field, 3 reared from nymphs), Tanzania, Uluguru Mts, 4 males, Tanzania, Nilo forest reserve, 2 males. *Gonatoxia maculata* Karsch 1889: Tanzania, Mt. Kilimanjaro, 17 males (1 collected in the field, 16 reared from nymphs). *G. immaculata* Karsch, 1889 Tanzania, East Usambara Mountains, Sigi Trail, 1 male, Tanzania, Kisarawe, Kazimzumbwi Forest Reserve, 1 male. *G. furcata* sp. n. /Hemp 2016 holotype.

Song measurements and sonograms were obtained using AMADEUS II and AMADEUS Pro (Martin Hairer; <http://www.hairersoft.com>). Oscillograms of the songs

were prepared using TURBOLAB (Bressner Technology, Germany). All recordings were made at temperatures between 20 and 27 °C. The singers were caged in plastic tubes, wire mesh cages or gauze cages with microphone fixed or hand held at distances between 5 and 60 cm. Data are presented as mean ± standard deviation.

Terminology. Syllable: sound produced during one cycle of movements (opening and closing of the tegmina), in *Gonatoxia* equivalent to a pulse; echeme: first order assemblage of syllables; pulse: undivided train of sound waves increasing in amplitude at the beginning and containing many similarly sized wave maxima and minima (cricket-like song structure; example see Fig. 20).

Chromosomes. *G. maculata* (eleven males and one female), *G. immaculata* (two males and two females), *G. furcata* sp. n. (one male) and *G. helleri* sp. n. (twelve males and seven females) were used for classical cytogenetic analyses. Chromosome preparation was obtained from adult gonads and gastric caeca. Testes, ovaries and gastric caeca were excised, incubated in a hypotonic solution (0.9% sodium citrate), fixed in ethanol - acetic acid (3:1, v/v) and stored at 2 °C until use. The fixed material was squashed in 45% acetic acid. Cover slips were removed by the dry ice procedure and then preparations were air dried. Constitutive heterochromatin was revealed by the technique as described by Sumner (1972). Chromosomes were classified on the basis of the criteria proposed by Levan et al. (1964). At least ten spermatogonial and/or oogonial metaphase and/or 20 meiotic divisions (diakinesis and metaphase I) per male, were analyzed.

Results

Taxonomy

Genus *Gonatoxia* stat. rev.

Karsch, 1889 [1888]. Berlin Ent. Z. 32: 423, 441.

Remarks. Massa (2015) synonymized *Gonatoxia* with *Dapanera* since the males of *Dapanera* and *Gonatoxia maculata* have a similar outer appearance and genitalic morphology. Massa discussed that morphological differences between the genera *Dapanera* and *Gonatoxia* given by Karsch (1889) are too small to rectify genus status. Differences between the both genera referred to the fastigium of vertex not being sulcate in *Gonatoxia*, sulcate in *Dapanera*, the tegmina wider in *Gonatoxia* compared to *Dapanera* and the genicular lobes of the hind femora wearing a spine in *Gonatoxia* and are unarmed in *Dapanera*. Massa (2015) discussed that also *Gonatoxia* has a sulcate fastigium verticis and *Dapanera* species may have a small spine on the genicular lobes. The only distinguishing character between both genera remaining as given by Karsch (1889) was tegmina width.

Until recently little material was available in museum collections from the two known species of *Gonatoxia*. Now specimens of *G. maculata* were collected on Mt Kilimanjaro (Hemp 2013a), fair numbers of this species

few months later in savanna habitats and deciduous dry forests around Mt Kilimanjaro and in the North Pare Mountains (Hemp 2013b). Since many more specimens were collected now from various Tanzanian localities and compared to the types and each other it became clear that the females of *G. maculata* and *G. immaculata* are very similar and the majority of collected specimens were without maculae on the tegmina. Males of *G. maculata* as well as of *G. immaculata* have maculae on the tegmina, but clearly differing in their genitalic morphology. Thus the name given by Karsch (1889) referring to the maculae on the tegmina is misleading since in both species males have well developed maculae. A third species, *G. furcata* sp. n. was detected in the Udzungwa Mountains clearly separated from the other species by a different colour pattern and the male genitalic system. *G. helleri* sp. n. is very similar to *G. maculata* and intensive studies on its acoustics were conducted to separate these two species which occupy different habitats. The four species exhibit a very uniform outer morphology, the females having stout, little serrated and strongly up-curved ovipositors while all species of the genus *Dapanera* also uniformly have a more elongated ovipositor (Fig. 1) strongly differing in shape from that in *Gonatoxias*. All *Gonatoxias* species are stout with a vivid yellow dorsal abdomen (Fig. 2B). The male genitalia of *Gonatoxias* are only superficially similar to those of the genus *Dapanera*. Thus genus status is justified by a very homogenous outer morphology of *Gonatoxias* species (Fig. 2) compared to *Dapanera* species. Therefore it is proposed to reinstate the genus *Gonatoxias*.

Gonatoxias maculata Karsch, 1889

Karsch. 1889[1888]. Berlin Ent. Z. 32:442.

Material studied. All Tanzania, 1 male, Mt Kilimanjaro, southern slopes, Msaranga valley, submontane riverine forest relicts, 1300 m, April 2011; 4 females, Mt Kilimanjaro, western slopes, Sanja Juu, 1300 m, savanna woodland May 2013; 3 males, 3 females, Mt Kilimanjaro, southern slopes, Rau forest near Moshi, lowland wet forest, 800 m, March, July, August, December 2014 and July 2015; 3 males, 4 females, North Pare Mountains, southern slopes, Lembeni, dry deciduous woodland, 1250 m, March, May, August 2013, May, November 2014 and July 2015; 1 female, Mt Kilimanjaro, southern slopes, Mabungu Hill, savanna woodland, 910 m, December 2013; 2 females, Mt Kilimanjaro, eastern slopes, Kirua, submontane savanna woodland 1300 m, July 2014; 1 female, Mt Kilimanjaro, eastern slopes, Holili, savanna woodland, 1300 m, June 2013 (collection C. Hemp).

Further material studied. 1 male, Somalia, Afgoi, Feb-March 1978, coll. A. Simonetta, B.M. 1979-543; 1 male, Kenya, Mombasa, coll. W. L. Slater, 1911-7. Depository NHML.

Description. Male. Males are characterized by a median deeply incised subgenital plate. The styli are long and slender and about 1.5 times longer than the medi-



Figure 1. Lateral view on ovipositor of female *Dapanera* sp. Uganda (NHML).



Figure 2. Habitus of *Gonatoxias* species. **A, B.** Male (A) and female (B) of *G. maculata*, Rau forest Kilimanjaro. Male with maculae on tegmina, female (B) showing the bright yellow tergites of abdomen, typical for all *Gonatoxias* species. **C.** Female *G. immaculata*, Kazimzumbwi Forest Reserve, Kisarawe near Dar es Salaam **D.** Female *G. furcata* sp. n., lowland forest Udzungwa Mountains, Morogoro District, Tanzania.

an incision (Fig. 3C). The cerci are stout, the tips wear a sclerotized ridge with numerous teeth (Fig. 3A, B). On the tegmina 2-6 white to ivory white patches are usually present which vary in number and size between the individuals (compare Fig. 2A). Teeth of stridulatory file at underside of left tegmen increase gradually in size (Fig. 4A) towards the anal end. Mirror area as in Fig. 5A, B.

Female. General habitus and colour. Predominantly green with broad oval tegmina and strongly up-curved ovipositor. Venation of tegmina often light green and often with tiny white dots scattered over tegmina, thus resembling a leaf perfectly. Whitish dots also on pronotum and legs. A pair of yellowish to whitish lines often present starting in upper part of compound eye and running over head and pronotum. Abdominal tergite bright yellow (2 B), tarsi whitish. **Head and antennae.** Antennae thin and whitish, surpassing tegmina. Eyes round, except for yellowish-whitish upper part green or brown-green. **Thorax.** Pronotal disc flat, longer posteriorly than pro-

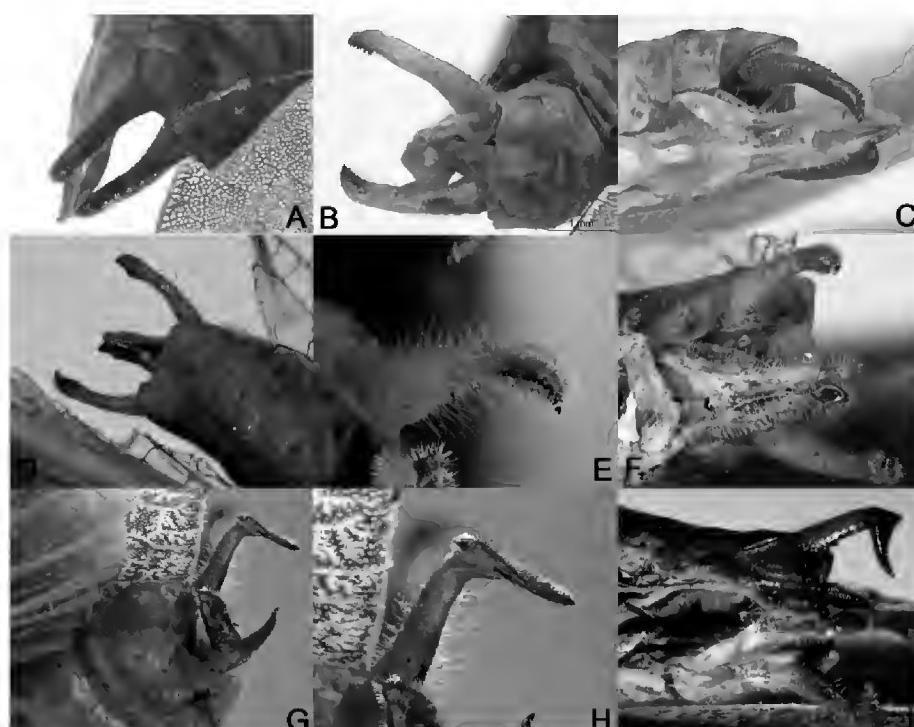


Figure 3. Morphological details of male *Gonatoxia* species. **A–C.** *G. maculata*, apex, semilateral view (**A**), dorsal view on cerci and apex (**B**), subgenital plate (**C**) **D–F.** *G. immaculata*, dorsal view on apex (**D**), right cercus (**E**), subgenital plate (**F**) **G–I.** *G. furcata* sp. n., semilateral view on apex (**G**), left cercus (**H**) and subgenital plate (**I**).

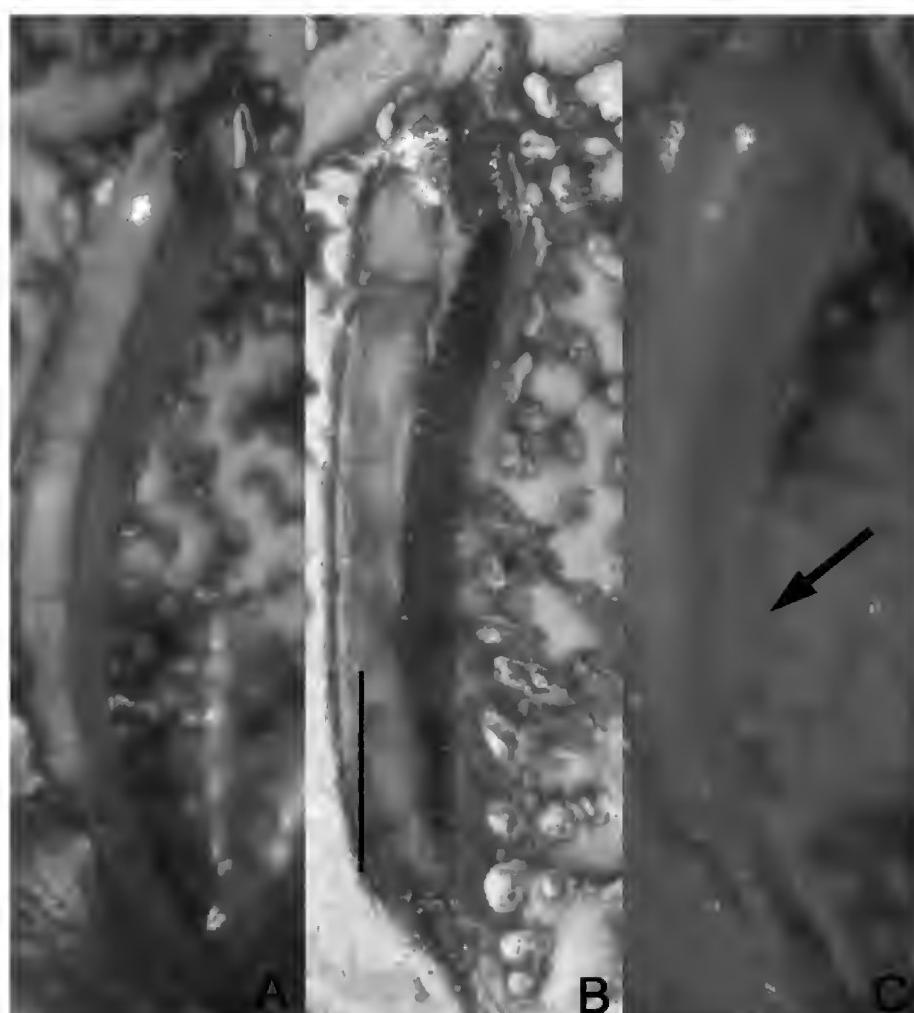


Figure 4. Stridulatory files of male *G. maculata* (**A**), *G. immaculata* (**B**) and *G. helleri* sp. n. (**C**). The arrow points to the discontinuity (elevation midway) typical for *G. helleri* sp. n. Scale bar 0.5 mm.

notal lobes which are evenly rounded at lower part, with acute edge at insertion of tegmina and wings. Tegmina broad with leaf-like pattern of veins, truncate at tips, alae surpassing tegmina. Alae hyaline except for tips which are of same green colour than tegmina. Stridulatory teeth on the right tegmen for female response to male calling song as in Fig. 6A. *Legs.* As in male. Fore femora with 3–4 outer spines, mid femora with 1–2 outer spines. Hind

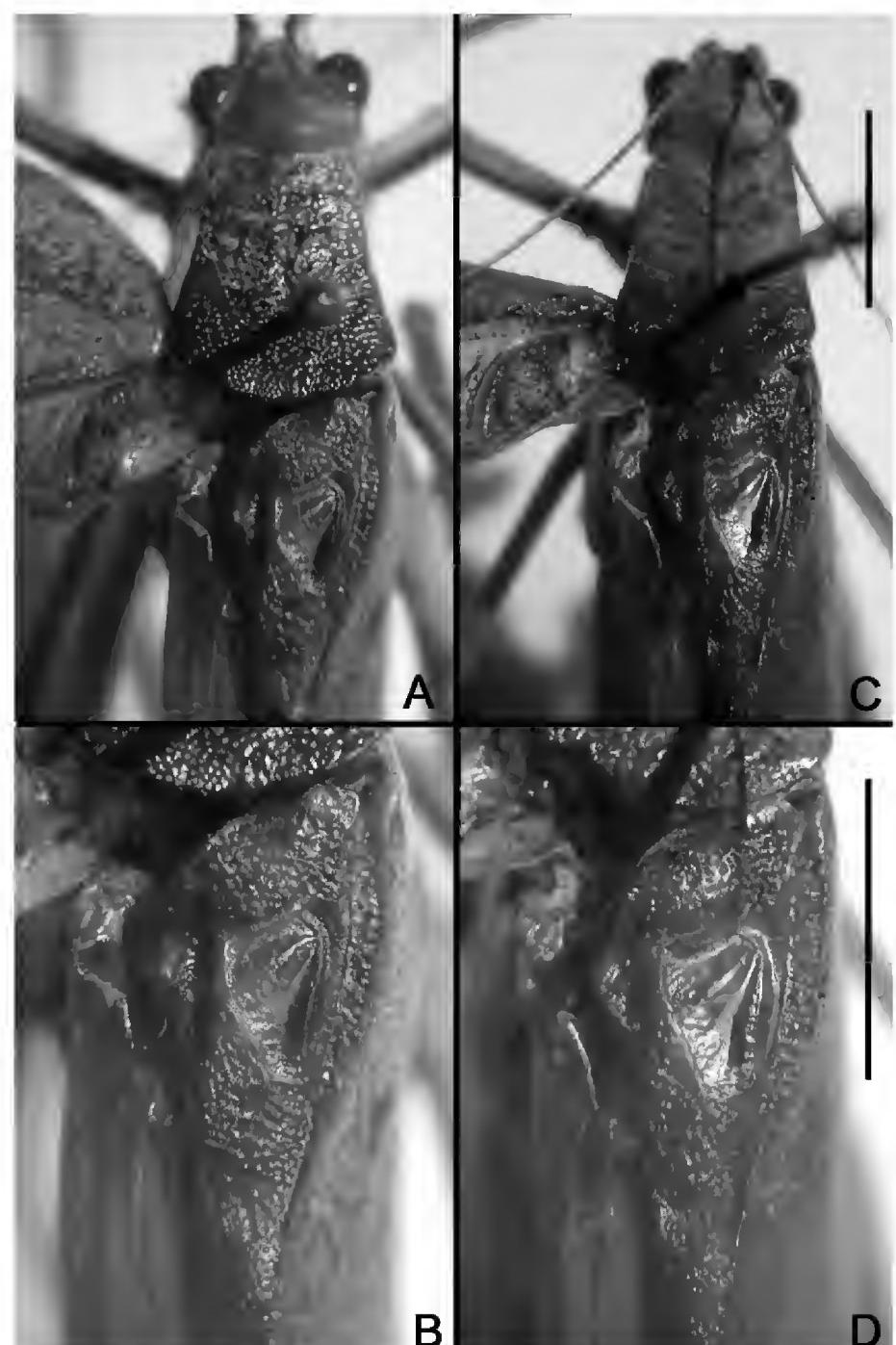


Figure 5. Pronotum and mirror area of male *G. maculata* (**A, B**) and male *G. helleri* sp. n. (**C, D**). Differences are small, the mirror of *G. helleri* sp. n. being more shiny and translucent. Scale bars 5 mm.

femora with 6–8 inner spines long whole length, outer side with 4–5 smaller spines at distal end of femur. Hind tibiae about length of hind femora, stout, in diameter almost tri-angular, curved. *Abdomen.* Plump abdomen with ovipositor strongly up-curved, valves at posterior third weakly sclerotized and serrated (Fig. 7A). Bowl-like structure lateral at base of ovipositor with strongly elevated lower margin, densely hairy in this region (Fig. 7A, 8A). Subgenital plate narrowly tri-angular (Fig. 9A). Cerci unmodified with stout base and slender elongated tip, strongly setose (Fig. 7A).

Nymphs. Nymphs similar to adults (Fig. 10A). When hatching recognized by curved hind tibiae (Fig. 11). Eggs are laid in rows glued to leaf tissue or along twigs (Fig. 12A, B).

Measurements (mm). **Females** ($n = 5$): Total length of body: 21.5–28.8; median length of pronotum: 6.1–6.3; length of hind femur: 26.2–27; length of tegmina: 41.8–44.7. Width of tegmina: 13.3–14.6; ovipositor: 5.3–5.8.

Since only data for the holotype male of *G. maculata* are available at present, we provide more measurement data.

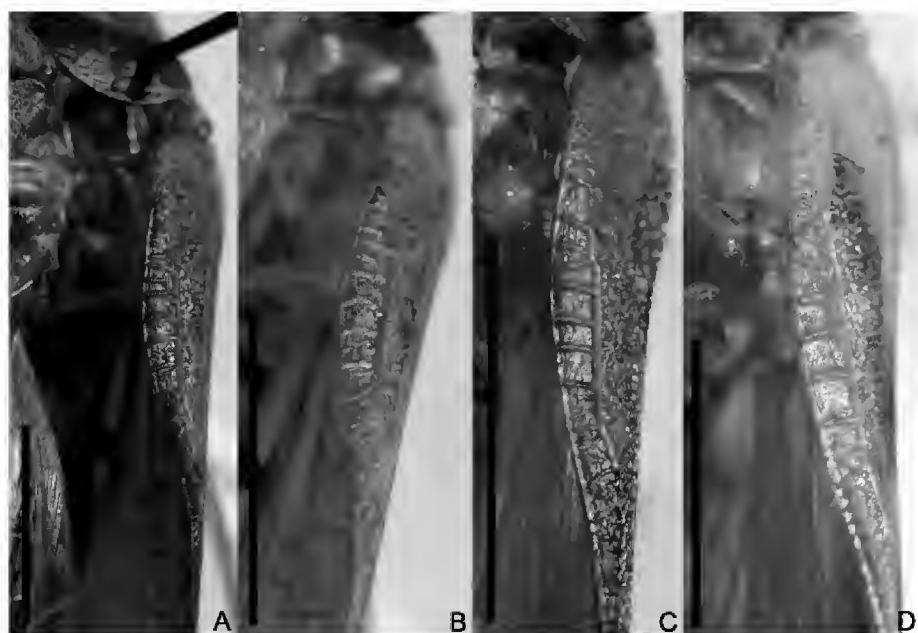


Figure 6. Right tegmen with stridulatory veins of female *Gonatoxias* species **A.** *G. maculata* **B.** *G. immaculata* **C.** *G. helleri* sp. n. **D.** *G. furcata* sp. n. Scale bars 5 mm.

Males (n = 8): Total length of body: 23–28 (holotype 30); median length of pronotum: 6.1–6.6 (holotype: 7); length of hind femur: 25–27 (holotype 25); length of tegmina: 41–43.7 (holotype 41); width of tegmina: 10.3–14 (holotype 11.5).

Biology. A pair from Kilimanjaro mated on the 19th of November 2014. Mating only took a couple of minutes. A spermatophore containing a two-parted spermatophylax was transferred to the female (Fig. 13). Two days later the female laid 26 eggs into the tissue or on the margin of a broad leaf (Fig. 12A). When offered leaves and dried twigs, females usually laid eggs in series on twigs (Fig. 12B). First eggs from a further female (mating was not recorded) hatched on the 31st of July 2015 (Fig. 11) and the first adult moulted on the 11th of October 2015. Thus development of nymphs takes about 2.5 months (laboratory conditions).

In two matings (one male, two females; interval about two months) of culture-reared specimens the male weighed 1584 and 1590 mg and the females 1950 and 1830 mg (all before mating) and the two-parted spermatophores 214 and 169 mg (each value mean of male weight loss and female weight gain).

Habitat. Savanna woodlands and deciduous dry forest up to submontane elevations.

Distribution. Tanzania, Kenya, Somalia.

Gonatoxias immaculata Karsch, 1889

Karsch. 1889[1888]. Berlin Ent. Z. 32:442

Material studied. Female Holotype, Usambara, MfN.

Further material studied. Tanzania: 1 male, 4 females, Pwani Region, Kisarawe District, Kazimzumbwi Forest Reserve, 150 m, February and July 2015. 2 males, East Usambara Mountains, Nilo forest reserve, December 2015 and May 2016; 1 male, East Usambara Mountains, Sigi Trail, 450 m, lowland wet forest, November 2015 (Collection C. Hemp). 1 female, Kenya, Rabai, coll. A.F.J. Geydte Jan-Feb 1929 (NHML).

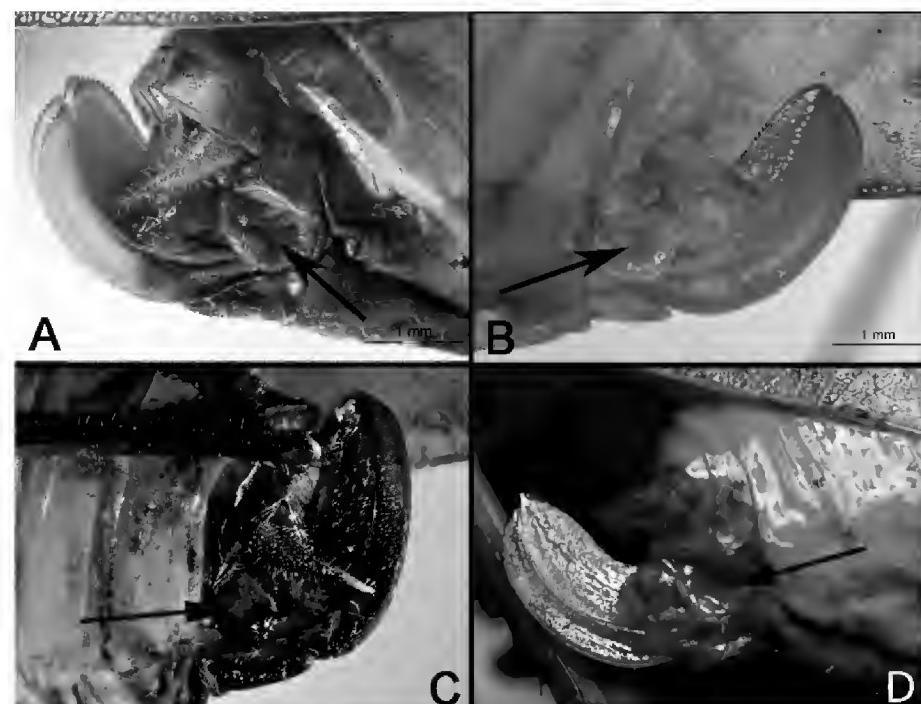


Figure 7. Lateral view on ovipositor of female *Gonatoxias* species. Note bowl-like structures laterally (arrows) **A.** *G. maculata* **B.** *G. immaculata* **C.** *G. furcata* sp. n. **D.** *G. helleri* sp. n. Scale bars 1 mm.

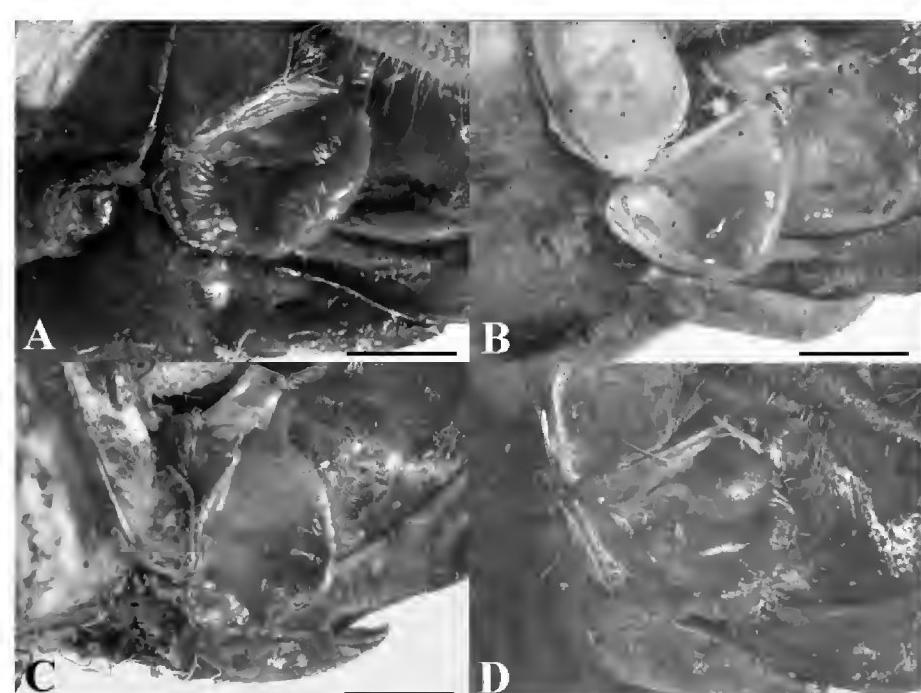


Figure 8. Bowl-like structures lateral at base of ovipositors of female *Gonatoxias* species. **A.** *G. maculata* **B.** *G. helleri* sp. n. **C.** *G. immaculata* **D.** *G. furcata* sp. n. Scale bars 1mm.

Description. Male. Color dark and shiny green, with few ivory to orange patches on tegmina; tergites of abdomen vivid yellow, venter whitish to light green; fore femora dorsally light brown, same colour as tarsi (Fig. 14). **Head and antennae.** Antennae thin, green, surpassing tegmina by about 1/3. Eyes round, brown-red. **Thorax.** Pronotal disc flat with sharp lateral edges, anterior margin v-shaped incurved, posterior margin of disc broadly rounded as described for genus (Karsch 1889). Lower margin of pronotal lobes broadly rounded, deeper than long, with sharp edge where wings are inserted. Tegmina broad, posterior end broadly truncate. Stridulation area tri-angle shaped flat on same level as pronotal disc as typical for genus. Stridulatory file as in Fig. 4B. Alae surpassing tegmina, in this area of same dark green shiny colour; with acute tips. Femora ventrally with spines. Fore tibiae slightly inflated in area of tympana. **Abdomen.** Last abdominal tergite with straight posterior margin (Fig. 3D). Cerci stout and setose; at tips

where serrated ridge starts slightly incurved (Fig. 3E), almost touching each other in alive insect. Subgenital plate with two short lobes, styli slightly inflated (Fig. 3F).

Female. Similar as male in habitus and colour. Stridulatory veins as in Fig. 6B. Ovipositor as in Fig. 7B. Bowl-like structure laterally on ovipositor more shallow as in *G. maculata* (Fig. 8C). Subgenital plate as in Fig. 9B.

Nymphs. Nymphs similar to adults (Fig. 10 B). Generally with a more shiny integument than in *G. maculata* (Fig. 10A) and with dorsal abdomen brown.

Measurements (mm). **Females** (n = 3): Total length of body: 23.8–25 (holotype: 27); median length of pronotum: 5.4–6.1 (holotype: 6); length of hind femur: 20–21.5 (holotype: 24); length of tegmina: 35.7–37.4 (holotype: 42). Width of tegmina: 12.1–12.6 (holotype: 14); ovipositor: 5–5.2 (holotype: 5).

Males (n = 2): Total length of body: 24–29; median length of pronotum: 6.2–6.7; length of hind femur: 21; length of tegmina: 36.2–42.3; width of tegmina: 11–13.5.

Remarks. When first males of *G. immaculata* were collected it became clear that specimens coming from Kazimzumbwi Forest Reserve belonged to *G. immaculata*. Thus the specimens from the spirit collection of the Zoological Museum Copenhagen listed as *G. maculata* from Kazimzumbwi Forest Reserve in Hemp (2013b) belong to *G. immaculata*.

Habitat. Lowland wet forest to submontane wet forest.

Distribution. Coastal Tanzania, East and West Usambara Mountains.

Gonatoxia furcata C. Hemp, sp. n.

<http://zoobank.org/47A84DC1-1D41-4BF5-AAF8-2F49618FF668>

Holotype male. Tanzania, Morogoro District, Udzungwa Mountains, National Park Headquarters, Mangula Gate, 300 m, lowland wet forest, July 2015. Depository MfN.

Paratype female, same data as holotype but March 2015. Depository MfN.

Further paratype material. 3 females, same data as holotype, May and June 2016 (collection C Hemp). 1 male (in alcohol), Tanzania, Iringa Region, Mufindi District, Udzungwa Scarp Forest Reserve, 08°31.5'S 35°53.9'E, 750 m, March 1996, McKamey et al. leg., depository ZMUC.

Diagnosis. Females of *G. maculata*, *G. immaculata* and *G. furcata* sp. n. are very similar. Differences are seen in the general coloration especially when specimens are alive. *G. maculata* and *G. helleri* sp. n. females are of lighter green colour while those of *G. immaculata* and especially *G. furcata* sp. n. are darker green and the tegmina shiny (Fig. 2B, C, D). The subgenital plate in *G. maculata* is not as broad as those of *G. helleri* sp. n., *G. immaculata* and *G. furcata* sp. n. (Fig. 9A, B, C, D) but the differences are not very pronounced. Lateral at the base of the ovipositors a bowl-like structure is present in all *Gonatoxia* species (arrows Fig. 7). In *G. maculata* this bowl-

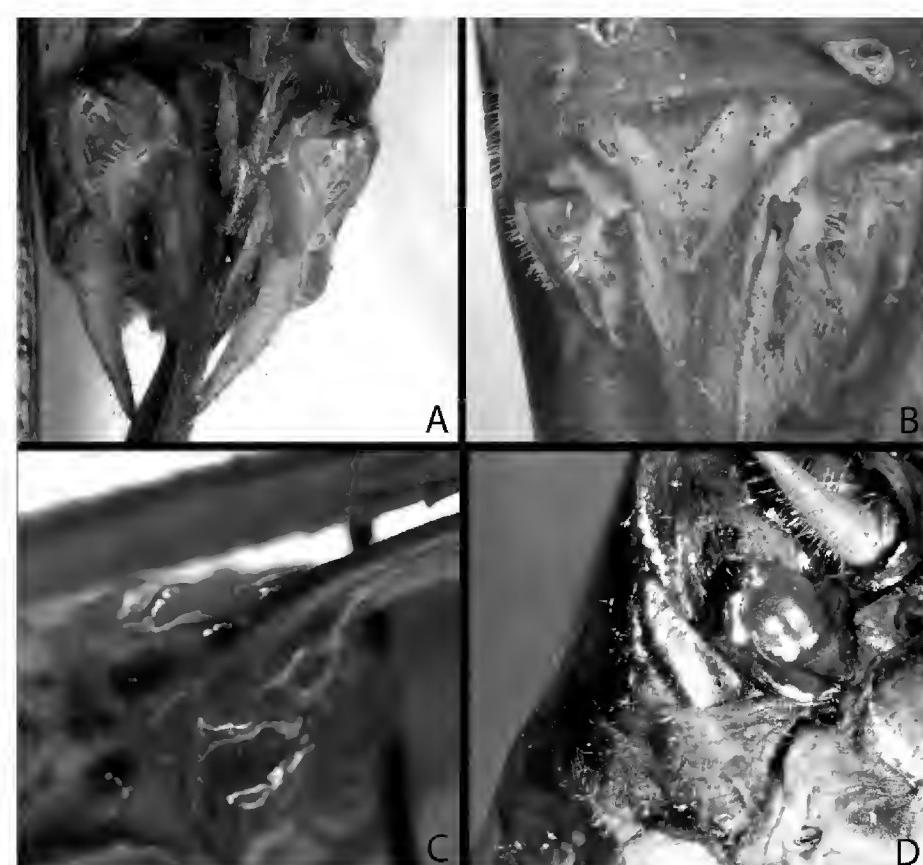


Figure 9. Subgenital plates of female *Gonatoxia* species. **A.** *G. maculata* **B.** *G. immaculata* **C.** *G. helleri* sp. n. **D.** *G. furcata* sp. n.

like structure is large and more deeply excavated than in *G. immaculata* (Fig. 8A). In *G. furcata* sp. n. inside the “bowl” a hump is located at the upper part and the lower margin is not hairy as in the other two species. The bowl-like structure in *G. helleri* sp. n. is very shallow and not as setose (Fig. 8B). Further *G. immaculata* females are smaller than those of *G. maculata* and *G. helleri* sp. n. while *G. furcata* sp. n. females are generally larger than those of the other three species.

Males are distinguished when comparing the outer genitalic morphology. In *G. maculata* the cerci are evenly tapering to their apices, the tips wearing a short and straight serrated ridge (Fig. 3B) while in *G. immaculata* the tips of the cerci wear a longer and curved serrated ridge (Fig. 3D, E). *G. helleri* sp. n. has similar built cerci as *G. maculata* but instead of a serrated ridge (Fig. 3B) a smaller ridge or 1–4 closely clustered teeth are located at the tips. In *G. furcata* sp. n. the tips of the male cerci are elongated, scythe-shaped with a very long serrated ridge (Fig. 3G, H, I). Males of all four species have maculae on the tegmina (Fig. 15). In *G. maculata* these white patches can be small or large and conspicuous, most specimens had 3–6 of these markings. In the known specimens of *G. immaculata* the patches were orange-brown (Fig. 14, 15C). The maculae of *G. furcata* sp. n. resemble those of *G. immaculata*, being orange-brown. *G. helleri* sp. n. usually has small longish white maculae and mostly not more than 2–4 (Fig. 15B, 16A).

Description. Male. Color dark and shiny green, with few ivory patches on tegmina; tergites of abdomen vivid yellow, venter whitish to light green; fore femora dorsally light brown, same colour as tarsi, thus similar to *G. immaculata*. **Head and antennae.** Antennae thin, green, surpassing tegmina by about 1/3. Eyes round, green, with light stripe beginning in eyes, running over the head getting yellow along lateral edges of the pro-



Figure 10. *Gonatoxia* nymphs. **A.** *G. maculata*, last instar **B.** *G. immaculata* 4th instar.



Figure 11. Hatching nymph of *G. maculata*.

notum. *Thorax*. Pronotal disc flat with sharp lateral edges, anterior margin v-shaped incurved, posterior margin of disc broadly rounded as described for genus (Karsch 1889). Lower margin of pronotal lobes broadly rounded, deeper than long, with sharp edge where wings are inserted. Tegmina broad, posterior end broadly truncate. Stridulation area tri-angle shaped flat on same level as pronotal disc. Stridulatory file evenly tapering in dent size. Alae surpassing tegmina, in this area of same dark green shiny colour; with acute tips. Femora ventral-

ly with spines. Fore tibiae slightly inflated in area of tympana. *Abdomen*. Last abdominal tergite with straight posterior margin (Fig. 3G). Cerci stout and setose; tips scythe-shaped with long serrated ridge (Fig. 3G, H, I). Subgenital plate with very short lobes, styli slightly inflated (Fig. 3I).

Female. Similar as male in habitus and colour (Fig. 2D) but with broader tegmina. Stridulatory veins as in Fig. 6D. Ovipositor as in Fig. 7C, subgenital plate as in Fig. 9C.

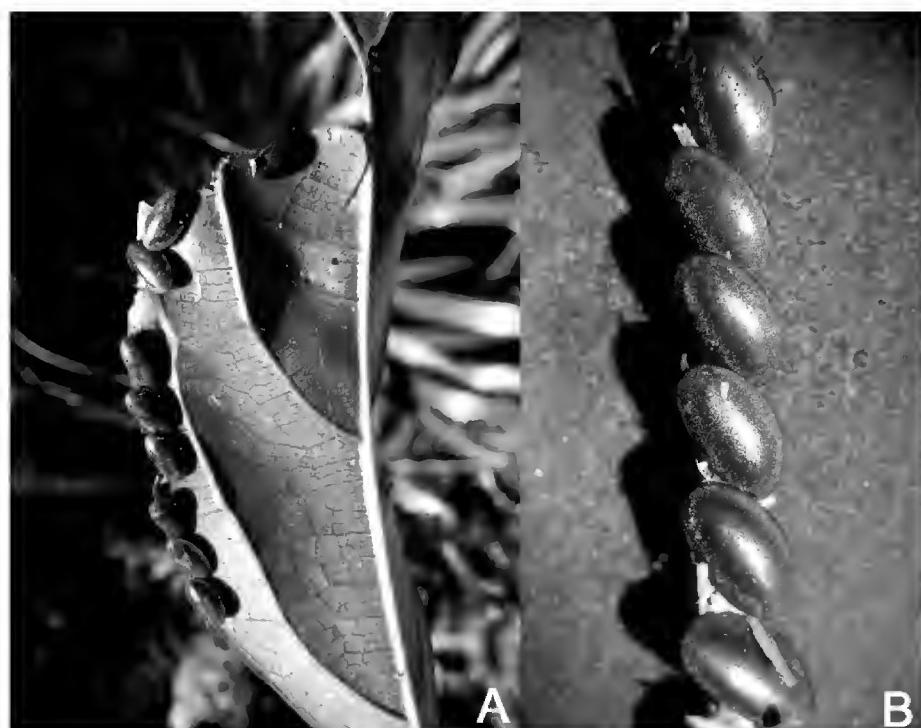


Figure 12. Freshly laid eggs of *Gonatoxia maculata* (A). 26 eggs were laid two days after mating and hatched 7 months later. (B) Eggs glued on a twig.



Figure 13. Pair of *Gonatoxia maculata* shortly after mating. Note the white spermatophore at the abdomen of the female.



Figure 14. *Gonatoxia immaculata* male, East Usambara Mountains. Note the orange patches on the tegmina and the deep green shiny colour.

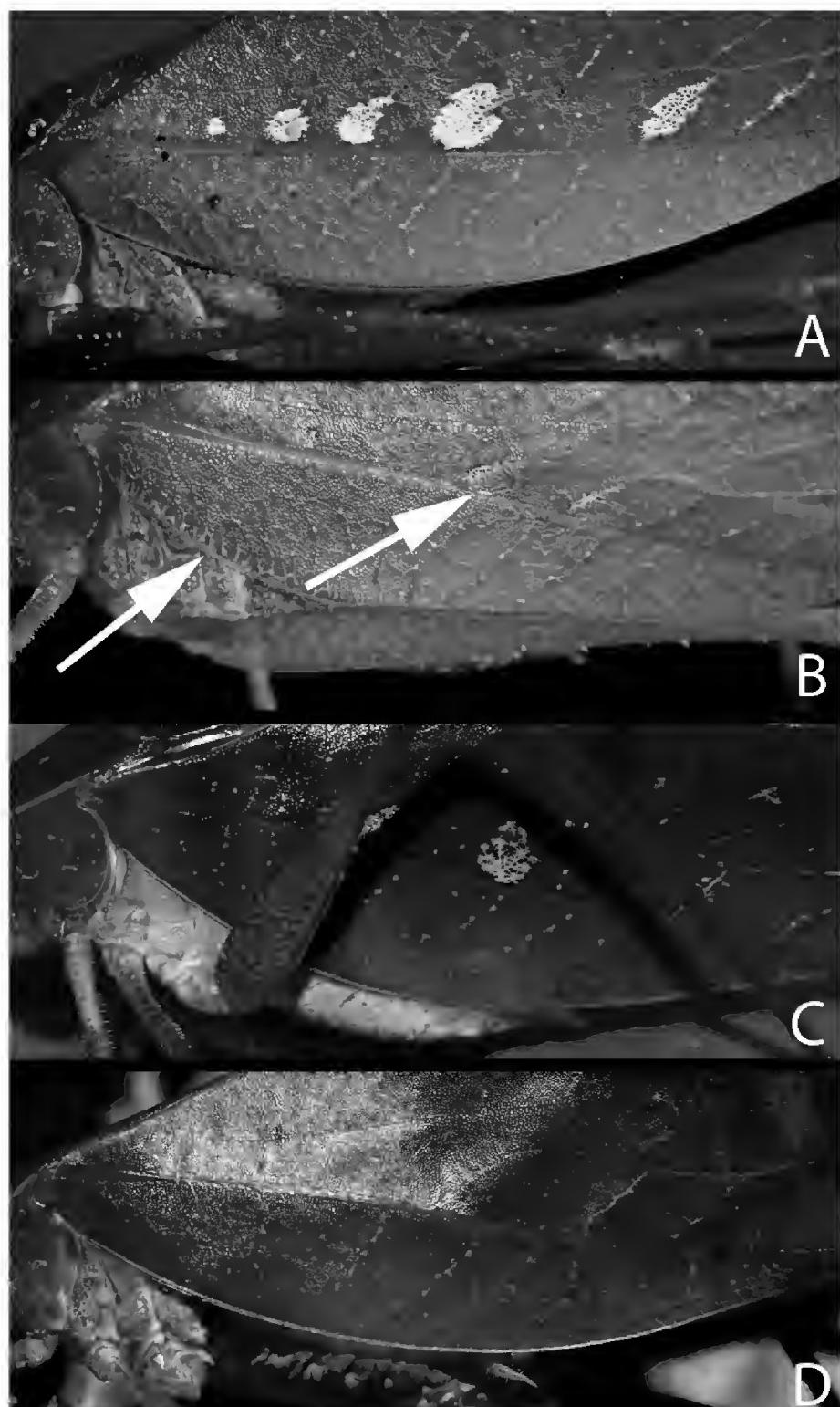


Figure 15. Left wings of male *G. maculata* (A), *G. helleri* sp. n. (B), *G. immaculata* (C) and female *G. furcata* sp. n. (D). Morphological differences between *G. maculata* and *G. helleri* sp. n. are small. However, usually *G. maculata* (A) have more and larger maculae on the tegmina while *G. helleri* sp. n. (B) have fewer maculae that are smaller and longish and usually start where *Rs* branches off (right arrow). Also *G. helleri* sp. n. has a white bordered costal margin with veins branching off white and thickened (left arrow).

Measurements (mm). **Females** (n=3). Total length of body: 26–27; median length of pronotum: 6.3–6.5; length of hind femur: 25–26.6; length of tegmina: 48–49; width of tegmina: 16; ovipositor: 5.5–6.

Males (n=1): Total length of body: 31.5; median length of pronotum: 6.9; length of hind femur: 25; length of tegmina: 43. Width of tegmina: 13.4.

Etymology. from Latin: *furca* = fork because of the forked male cerci.

Habitat. Lowland wet forest.

Distribution. At present only known from the Udzungwa Mountains, Tanzania.

Gonatoxia helleri C. Hemp, sp. n.

<http://zoobank.org/9BA1D6AD-AA58-4706-B93C-CF9FC2D94438>

Holotype male. Tanzania, Uluguru Mountains, Morogoro District, forest above Morningside, February 2016. Depository MfN.

Paratype female, same data as holotype; depository MfN.

Further paratypes. All Tanzania; 13 males, 17 females, same data as holotype, March and April 2016; 3 males, 1 female, East Usambara Mountains, Nilo forest reserve, February and May 2016; 1 male, East Usambara Mountains, Sigi Trail, lowland wet forest, 450 m, November 2015; 1 male, 4 females, West Usambara Mountains, Lutindi Mental Hospital, submontane forest, 1250 m, February 2015 and June 2016; 1 male, 1 female, West Usambara Mountains, Mazumbai forest reserve, 1600 m, March 2016; 7 males, 3 females, Udzungwa Mountains National Park, Mangula Gate, lowland wet forest, 300 m, March, July, September 2015, January, March and May 2016; 1 female, Kisarawe District, Kazimzumbwi Forest Reserve, February 2015 (collection C. Hemp).

Further material studied. 1 male, Kenya?, Kibatuga, 20/10/51, B.M 1966–628; 1 female, East Africa 82/24, Tanzania, Korogwe-Msata Road, 103 km north of Msata, summit of kopj, 21 IX 1982, coll. N. Jago; 1 female, Tanzania, Kilosa. 10 IX 1926, coll. N. C. E. Miller, B.M. 1928–281; 1 female, Tanzania 63, B.M. 1950–96; 1 female, Tanzania, Lindi, Ndanda, 300 m, 5. III 1952, coll. Lindemann and Pavlitzki; 1 male, N Derema, coll. G. v. Son, B.M. 1969–331 (depository: NHML). The specimens from the collection of the NHML are not listed as paratypes since they were either females that are difficult to identify without males or males where the stridulatory file could not be studied.

Diagnosis. *G. helleri* sp. n. is very similar to *G. maculata*. Both species have about the same size and colour and shape of tegmina and wings. However, *G. helleri* sp. n. usually have far less conspicuous maculae on the tegmina, being smaller and more longish and fewer in number. Mostly these maculae start about where the Rs vein branches off. Typical is also a dense net of white veins, especially in the costal area of the tegmen forming multiple small white dots. Also the costal margin is bordered white with veins branching off thick and very white in both sexes when alive (weakly expressed in the Udzungwa population of *G. helleri* sp. n.). The males of *G.*

helleri sp. n. can also be distinguished from *G. maculata* by in the male cerci wearing a smaller sclerotized ridge or 1–4 single teeth clustered tightly together whereas *G. maculata* males wear a stouter and larger serrated ridge at the tips of the male cerci. Differences are also seen in the stridulatory file of the males. The stridulatory file of *G. maculata* evenly tapers in dent size from one side to the other (Fig. 4A) while in *G. helleri* sp. n. the stridulatory file is somewhat constricted and elevated midway with larger teeth following running to the margin of the left tegmen (Fig. 18; Fig. 4C, arrow) and thus dividing the whole structure into three parts. *G. helleri* sp. n. has a male subgenital plate which is not as deeply incised as in *G. maculata* and the styli are flattened and broad (Fig. 17C) while in *G. maculata* the subgenital plate is deeper incised and the cerci longer and more stout (Fig. 3C). *G. immaculata* and *G. furcata* sp. n. both are shiny dark green usually, *G. immaculata* males often have conspicuous white to orange patches on the tegmina. The cerci of male *G. immaculata* have a sclerotized curved ridge at their tips while *G. furcata* sp. n. males have scythe-shaped cerci. The females are often difficult to identify since also more light green individuals of *G. immaculata* occur and the shiny colour vanishes in preserved specimens. Further *G. helleri* sp. n. was found syntopically with *G. immaculata* in the East Usambara Mountains. In the Udzungwa Mountains *G. helleri* sp. n. occurs syntopically with *G. furcata* sp. n. However, *G. furcata* sp. n. females are generally larger than *G. helleri* sp. n. females and of shiny dark green colour. *G. immaculata* females are difficult to distinguish from *G. helleri* sp. n. females and only the study of larger series comparing the bowl-like structure laterally on the ovipositor may help to identify females of both species, especially in preserved specimens.

Description. Male. General habitus and colour. Predominantly green with oval tegmina and 2–4 small ivory

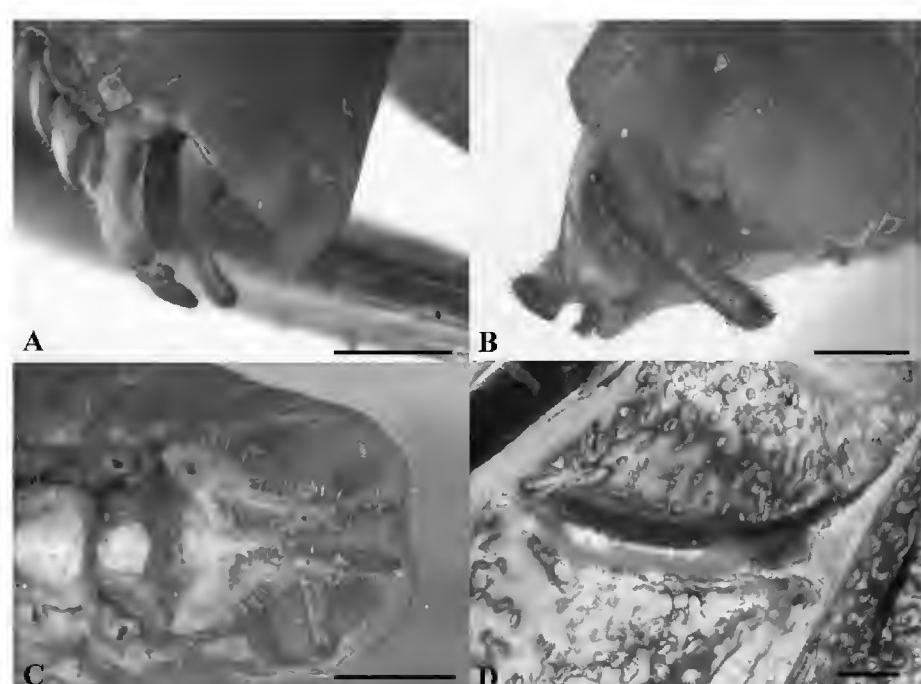


Figure 17. Morphological details of male *Gonatoxia helleri* sp. n. A. Semilateral view on abdominal apex. Scale bar 1 mm B. Dorsal view on abdominal apex with sclerotized ridge of cercus. Scale bar 1 mm C. Subgenital plate. Scale bar 1 mm D. Stridulatory file. Scale bar 500 µm.

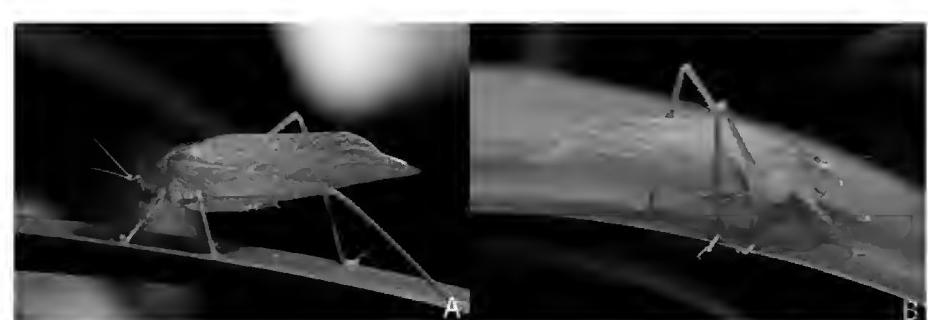


Figure 16. *G. helleri* sp. n., male (A) and female (B) from the Uluguru Mountains.

patches on tegmina (Fig. 16A). Whitish dots also on pronotum and legs. Pair of white lines often present starting in upper part of compound eye and running over head and pronotum. As in all *Gonatoxias* species abdominal tergite bright yellow, tarsi whitish. *Head and antennae*. Antennae thin and whitish, surpassing tegmina. Eyes round, except for whitish upper part green or light green. *Thorax and wings*. Pronotal disc flat, longer posteriorly than pronotal lobes which are evenly rounded at lower part, with acute edge at insertion of tegmina and wings. Tegmina broad with leaf-like pattern of the veins, slightly truncate at tips, alae surpassing tegmina. Alae hyaline except for tips which are of same green colour than tegmina. Tegmina with net of white veins, on veins often white dots are formed, especially in costal area (Fig. 15B). Costal margin white bordered with veins directly branching off at margin thick and white. Stridulatory file (Fig. 17D) separated into three parts with small teeth near tegmen base, an elevation midway (arrow Fig. 4C) and large teeth at outer part of file. *Legs*. Fore femora with one outer spine and 1–4 inner spines ventrally. Mid femora with 3 outer and no inner ventral spines. Hind femora with double row of irregular set of 7–8 ventral spines. Fore tibiae in area of tympana slightly enlarged, with conchate inner tympanum and open oval tympanum on outer side; midway dorsal one spine, ventral several irregular set spinules. Mid tibiae with irregular set spinules in four rows. Hind tibiae dorsally two ridges densely covered by small spines, ventral side with few

irregular set spines, curved. *Abdomen*. Venter white. Cerci slender and incurved (Fig. 17A, B), at tips with short ridge or 1–4 single sclerotized dents. Subgenital plate medially u-shaped incised, styli flat, roundish and somewhat inflated, touching each other medially when insect is alive (Fig. 17C).

Female. Similar to male in size but with more roundish tegmina and mostly without ivory patches on tegmina or 1–2 and very small ones, mostly where Rs branches off. Also with for this species typical costal margin bordered white with branching off veins thicker and white and net of white veins forming white dots. Stridulatory veins as in Fig. 6C. Ovipositor up-curved, serrated at tip (Fig. 7D). Bowl-like structure formed laterally on base of ovipositor as in Fig. 8B. Subgenital plate tri-angular (Fig. 9C).

Body mass. (mg; n=1) Male 990. Female 1462 (culture-reared, 01.08.2015).

Measurements (mm). **Females** (n=6): Total length of body: 25.8–27.5; median length of pronotum: 6.5–6.8; length of hind femur: 26.5–28.6; length of tegmina: 44.0–45.9; width of tegmina: 14.8–14.4; ovipositor: 5.2–5.4.

Males (n=6): Total length of body: 23.5–26.4; median length of pronotum: 5.7–6.5; length of hind femur: 25–28; length of tegmina: 42.5–44.4; width of tegmina: 12.5–13.4.

Etymology. Named after Klaus-Gerhard Heller.

Habitat. Lowland wet to submontane forest.

Distribution. Tanzania and very likely Kenya.

Key to males of *Gonatoxias*

- | | | |
|---|---|--------------------------|
| 1 | Male cerci not scythe-shaped | 2 |
| – | Male cerci scythe-shaped (Fig. 3G, H)..... | <i>G. furcata</i> sp. n. |
| 2 | Male subgenital plate deeply medially incised, styli long and slender, about 1.5 times as long as incision (Fig. 3C) | <i>G. maculata</i> |
| – | Male subgenital plate not deeply medially incised, styli not longer than incision, broader and compressed..... | 3 |
| 3 | Cerci with short straight sclerotized ridge at tips (Fig. 17B); subgenital plate u-shaped incised forming stout lateral processes and oval slightly compressed styli (Fig. 17C) | <i>G. helleri</i> sp. n. |
| – | Apices of male cerci inwardly curved and with long sclerotized serrated ridge (Fig. 3 E) | <i>G. immaculata</i> |

Bioacoustics

Morphology of stridulatory organs: In the male, the slightly curved stridulatory file (Fig. 4) is found on the underside of the left tegmen, carrying between 50 and 60 teeth. On the corresponding place of the right tegmen there is a similar sized (non-functional) file. At the anal end there is no trace of a lump or comparable structure. On the contrary, the file starts with a few weakly sclerotized teeth, which lead up to the elevated main part of the file. Here the steep side of the teeth is directed towards the anal end (Fig. 18; see Discussion). The inter-tooth intervals in *G. maculata* (n=2), *G. immaculata* (n=2) and *G. furcata* sp. n. (Holotype) decrease more or less continuously from 50 µm at anal end to 30 µm near the articulation (Fig. 19). In *G. helleri* sp. n. however, there is a discontinuity

in the middle (see arrow in Fig. 4C), and the intervals in the basal part are around 55 µm (n=3). For function of this file part see Heller and Hemp, in prep. The mirror is relatively small and inconspicuous (Fig. 5), in *G. helleri* sp. n. a little bit more glossy than in *G. maculata*.

The females bear one distinct row of spines on each of several veins on the upper side of the right tegmen (Fig. 6; about eight in *G. maculata*) as it is typical for acoustically responding phaneropterine females (Heller et al. 2015).

Spectral composition of song: The frequency spectra of the male songs were relatively narrow-banded in all four species studied (for example see Fig. 20). In *G. maculata* the peak is between 12.6 and 17.4 kHz (n=17), in *G. immaculata* between 17.0 and 23.6 kHz (n=2), in *G. fur-*

cata sp. n. 16.9 kHz (n=1) and in *G. helleri* sp. n. between 15.6 and 20.8 kHz (n=7). The bandwidth 10 dB below the peak was always between 1.3 and 3.9 kHz. All data refer to the first syllable of a pair of syllables (see below).

Song pattern. The calling songs of all studied species consisted of short (1–4 ms), resonant syllables (Fig. 21), often emitted in pairs. Comparing the grouping of these syllables or syllable pairs, the species can be separated into two groups. The first group consists of *G. maculata* and *G. helleri* sp. n. Isolated physically and acoustically, the males of these species produced long sequences of pulses. These series typically lasted 30 to 90 seconds and were separated by intervals of many minutes. Within a sequence, *Gonatoxia maculata* nearly always emitted pairs of pulses with intra pair intervals of about 70 ms and inter pair intervals of 2 s. In the song of *G. helleri* sp. n. pairs of pulses and single pulses were found, with intra pair

intervals as in *G. maculata* and intervals between pairs/single syllables ca. 0.3–1 s. Additionally, in many recordings of both species stereotypic combinations of pulses were found, where an additional pulse (or a very dense pulse group) following after a pair (or in *G. helleri* sp. n. sometimes a single pulse) in an interval of about 250 ms. These combinations belong to the acoustical male-female-interactions and will be treated in a separate paper (Heller and Hemp, in prep). The males of the second group, consisting of *G. immaculata* and *G. furcata* sp. n., produced much shorter syllable series, lasting only a few seconds, and the intervals between the syllable pairs were also much shorter than in the first group. In *G. immaculata* the intra-pair interval was about the same as in the song of the members of the first group. However, both recorded males showed distinct differences concerning the inter-pair intervals and the frequency of single pulses. In *G. furcata* sp. n., the intra-pair interval was with about 120 ms distinctly larger than in the other three species. In this species, some of the short series followed each in relatively short intervals.

Cytotaxonomy

Comparison of the chromosomes of four *Gonatoxia* species revealed differences between their karyotypes, including the number of chromosomes (2n), the morphology of the chromosomes, the fundamental number of chromosome arms (FN) and C-banding patterns. All analyzed species show the same sex determining system: X0 (male) and XX (female) as well as the acrocentric X chromosome which is the largest element of the set.

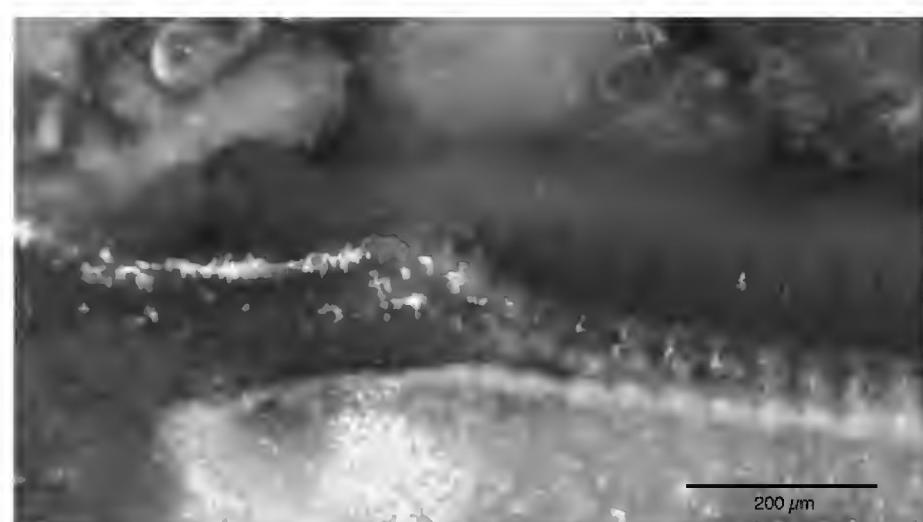


Figure 18. Detail of stridulatory file of *Gonatoxia immaculata* with teeth directed towards the anal end.

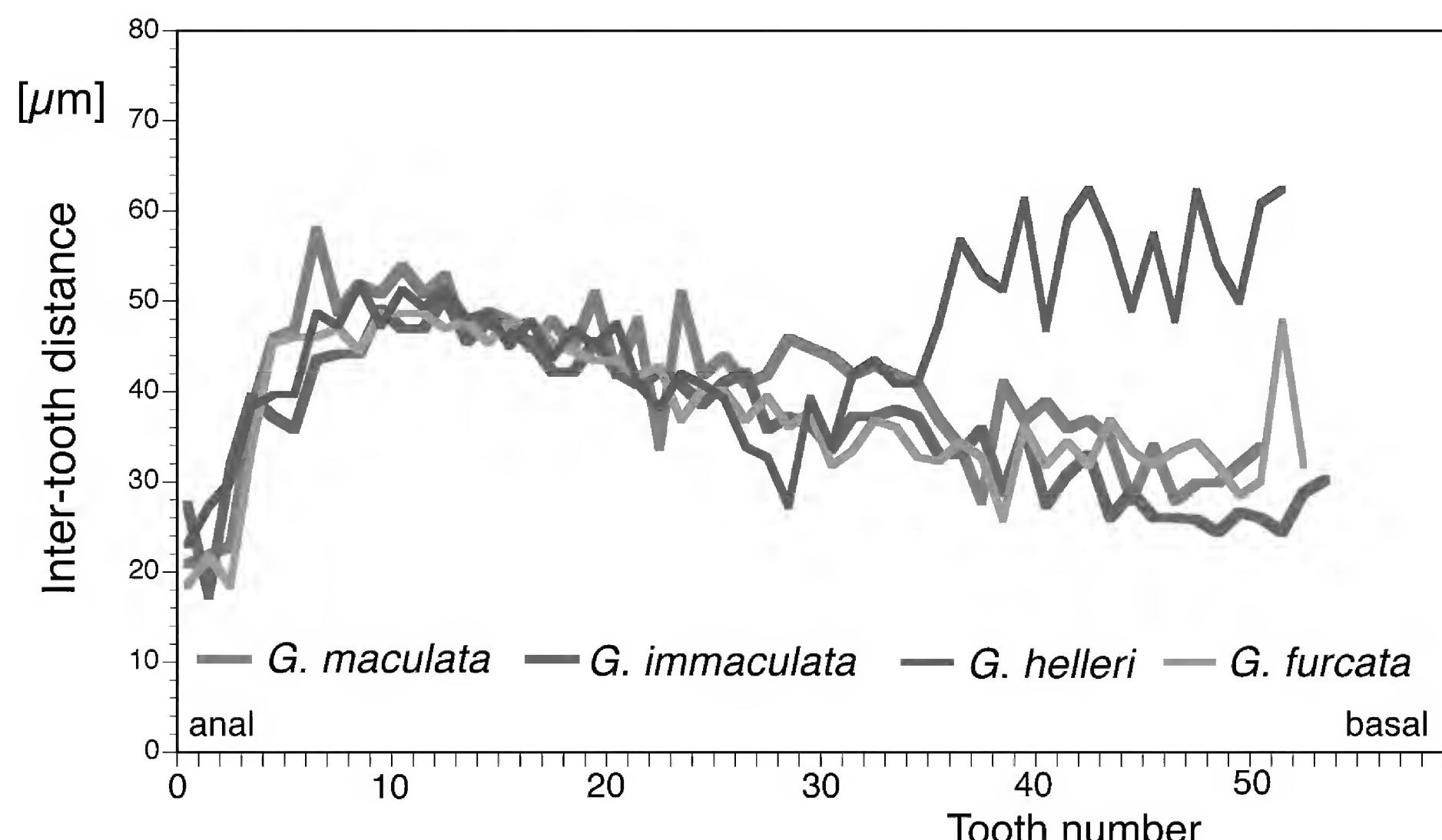


Figure 19. Inter-tooth spacing in stridulatory files of male *Gonatoxia* species (most intervals between small teeth at the anal end not measured).

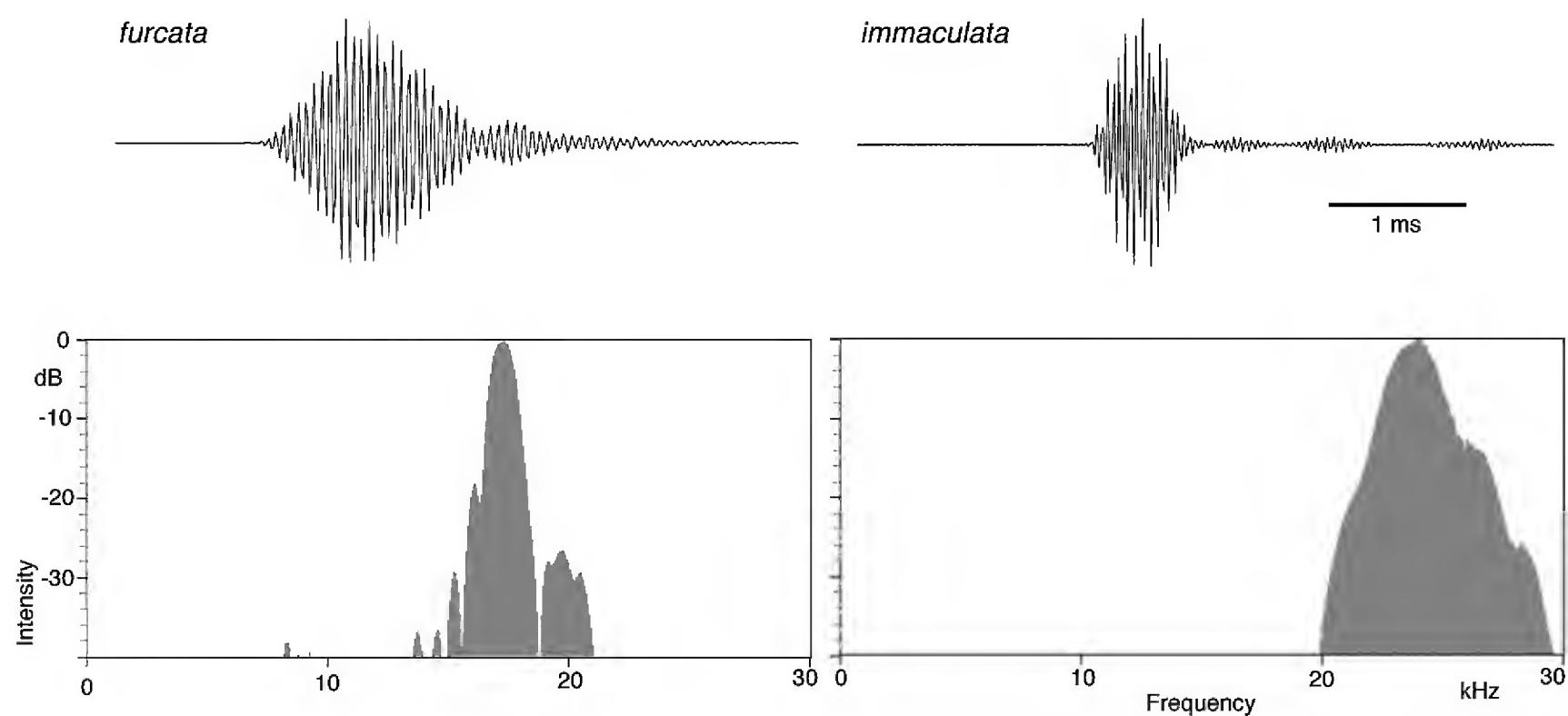


Figure 20. Oscillograms of single syllables of the male calling song and corresponding spectral composition (power spectra).

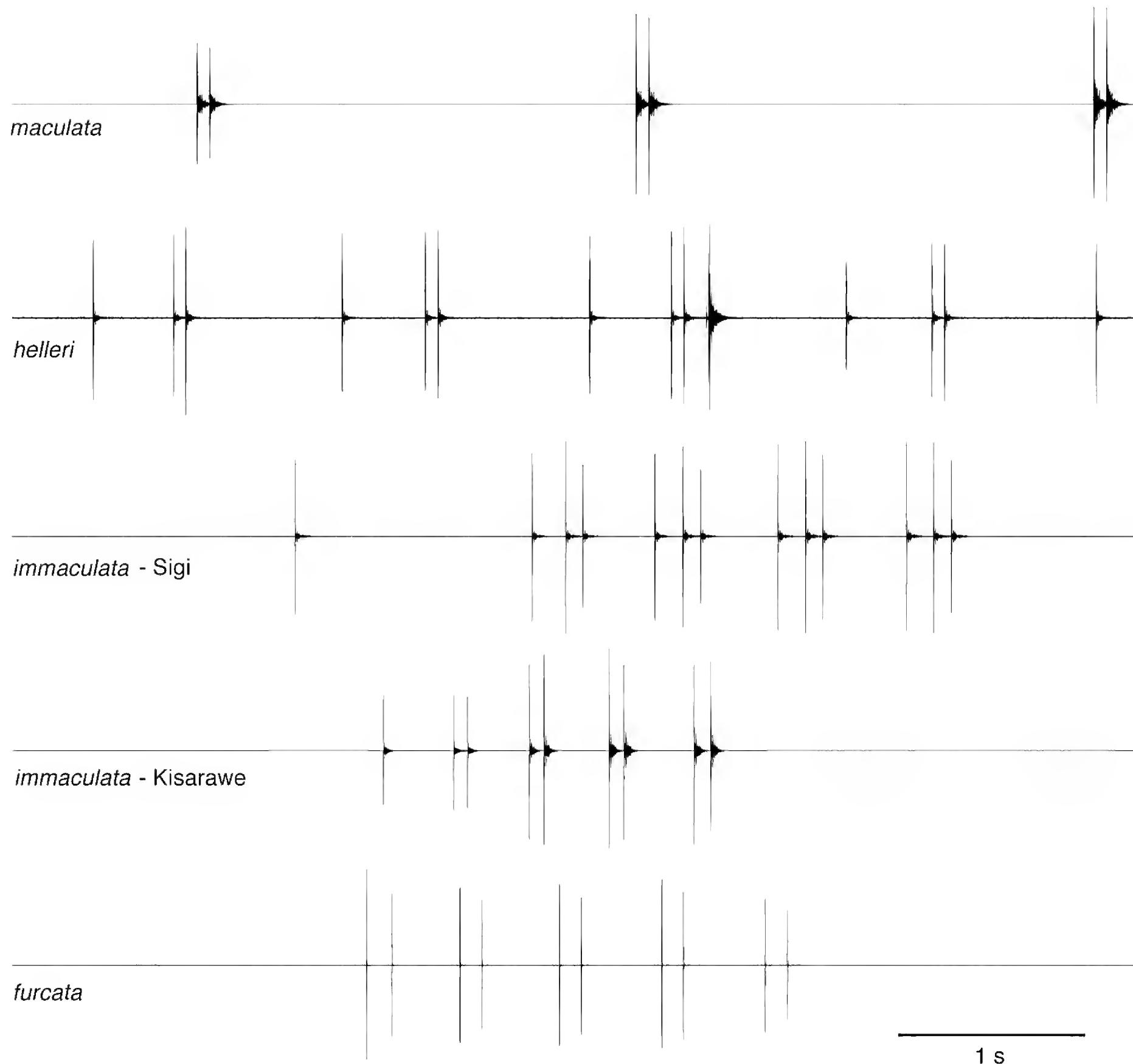


Figure 21. Oscillograms of the male calling song of *Gonatoxia* species. In *G. maculata* and *G. helleri* only part of a much longer sequence is shown, in *G. immaculata* and *G. furcata* complete series.

The standard karyotypes of *G. maculata* and *G. immaculata* were characterized by a chromosome number of $2n = 29$ (males) and 30 (females). All chromosomes were acrocentric, consisting of three long, four medium and seven short pairs (Fig. 22A, B). In the single male investigated of *G. furcata* sp. n. (Fig. 22C) and one male of *G. maculata* from North Pare Mts, Lembeni the chromosomal number was reduced to $2n = 27$; one medium pair was metacentric ($\text{FN} = 29$), whereas in second one probably acrocentric (not shown). One male of *G. immaculata* had mosaic cells with 29 and 27 chromosomes. C-banding revealed some differences in number and distribution of constitutive heterochromatin blocks (C-bands) between and within species (Fig. 22).

The study of spermatogonial, oogonial and somatic gastric caeca mitotic metaphase of *G. helleri* sp. n. showed in most cells 7 chromosomes, $\text{FN} = 10, 11$ in the male (Fig. 22D, F, G) and 8, $\text{FN} = 11, 12$ in the female (Fig. 22E). In all individuals the first long pair was meta/submetacentric, whereas the second long pair was polymorphic and characterized by three main karyomorphs (A, B, C) in respect to the morphology of homologous chromosomes and heterochromatin patterns of C-bands among analyzed specimens: (A) eight samples from the Udzungwa Mts and four from the Eastern Arc Mountains (Nilo forest reserve) presented meta- or submetacentric chromosomes in a homozygous or heterozygous state (Fig. 22D, E); (B) five individuals from the Udzungwa Mts and two coming from the Uluguru Mountains showed meta/submetacentric and acrocentric chromosomes (Fig. 22F); (C) one single male collected in the Uluguru Mts had homologous acrocentric chromosomes (Fig. 22G). After C-staining, chromosomes of this pair and in the third acrocentric pair showed quantitative variation in heterochromatin blocks among the analyzed individuals.

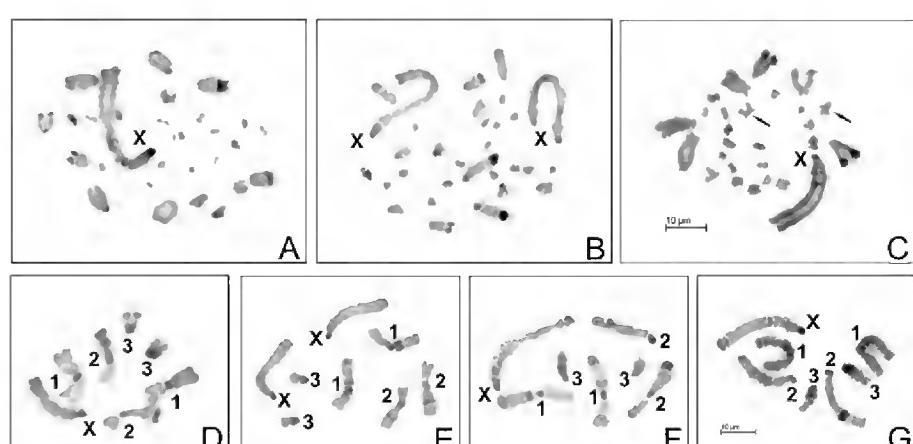


Fig 22. C-banded mitotic metaphase of male complement of *G. maculata* (A), female *G. immaculata* (B), male *G. furcata* sp. n. (C) as well as both male (D, F, G) and female (E) of *G. helleri* sp. n. Arrows indicate biarmed chromosomes in *G. furcata* sp. n. (C). In *G. helleri* sp. n. the long polymorphic pair 2 shows three main karyomorphs in which homologous chromosomes differ in their morphology: both meta- or submetacentric (D, E), meta/submetacentric : acrocentric (F) and both acrocentric (G). X, sex chromosome. Scale bar = 10 μm .

Discussion

Taxonomy

Four species of *Gonatoxia* are known at present. However, further specimens stored in the entomological collection of the Natural History Museum in Vienna probably belong to new species of *Gonatoxia*. One male is labelled “Zanzibar”, collected by A. Horn, showing cerci with only single sclerotized dents at their tips and an unlobed subgenital plate with short styli. Until further material gets available we decided not to describe this new species.

Another male specimen identified as “*Arantia spinulosa*” collected by A. Horn also belongs to *Gonatoxia*. This specimen is labelled “MKaffa”, could thus come from Ethiopia. It is larger than *G. maculata* which it resembles in terms of male cerci, tegmina shape and maculation (Fig. 23). Since the locality is not clear further specimens have to be collected to clarify where this specimen is coming from and whether it belongs to a new species of *Gonatoxia*.

Further two specimens in Vienna were also studied, collected by Reimer labelled “DO Afrika” thus coming from Tanzania. Since the exact locality is unclear and the cerci could not be studied in detail without damaging the very old specimens a diagnosis to which species they belong is uncertain. One of the two males, however, could belong to *G. immaculata* since the subgenital plate agrees with males collected from the East Usambara Mountains and Kazimzumbwi Forest Reserve, the other to *G. maculata*. For the distribution of *Gonatoxia* species in East Africa see Fig. 24.

Studying a larger series of *Gonatoxia* specimens newly collected in Tanzania and from the entomological collections of Vienna and London showed that *Gonatoxia* is a very uniform genus and well separated from *Dapanera* which it superficially resembles. However, molecular studies on *Dapanera* and *Gonatoxia* are necessary to deepen our understanding about generic relationships, also on tribal level within Holochlorini.

Bioacoustics

The calling song of all four species of *Gonatoxia* consists of very short, cricket-like, resonant syllables, separated by large silent intervals, similar as in the genus *Parapryrrhicia* Brunner von Wattenwyl (Hemp et al. 2016). The duty cycle (percentage of time with actual sound emission) of these songs is obviously very low, and singing males are certainly difficult to detect by acoustically orienting predators or parasitoids (for a more detailed discussion of the advantages of this song type see Hemp et al. 2016).

However, the structure of the stridulatory file of *Gonatoxia* differs somewhat from that of *Parapryrrhicia*. The distribution of the inter-tooth intervals is similar, but from the anal end onwards the file runs on a slightly elevated bulge and the teeth are larger. In the larger teeth it is

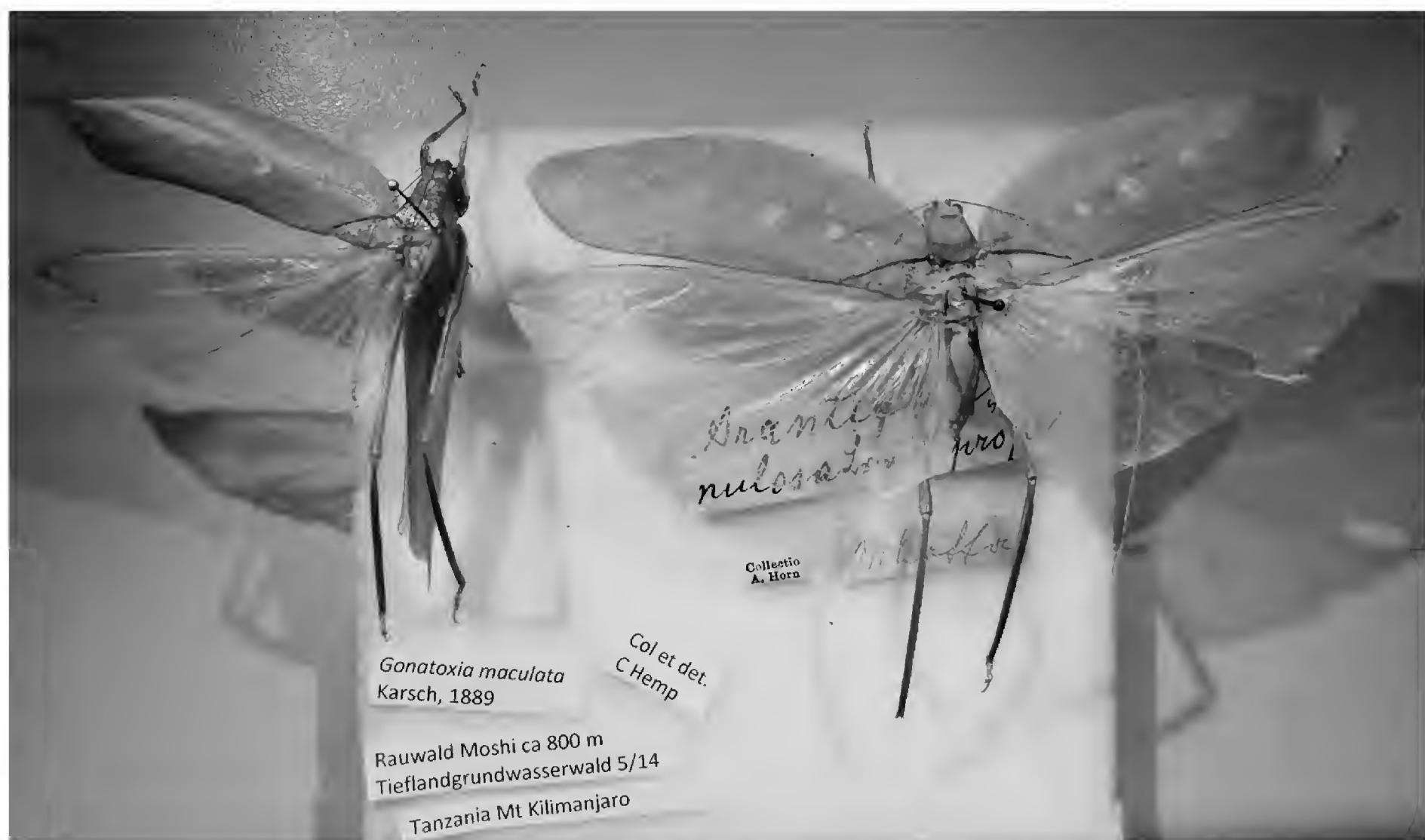


Figure 23. Comparison of *G. maculata* male from Mt Kilimanjaro with specimen in the collection of Vienna labeled *Arantia spinulosa*.

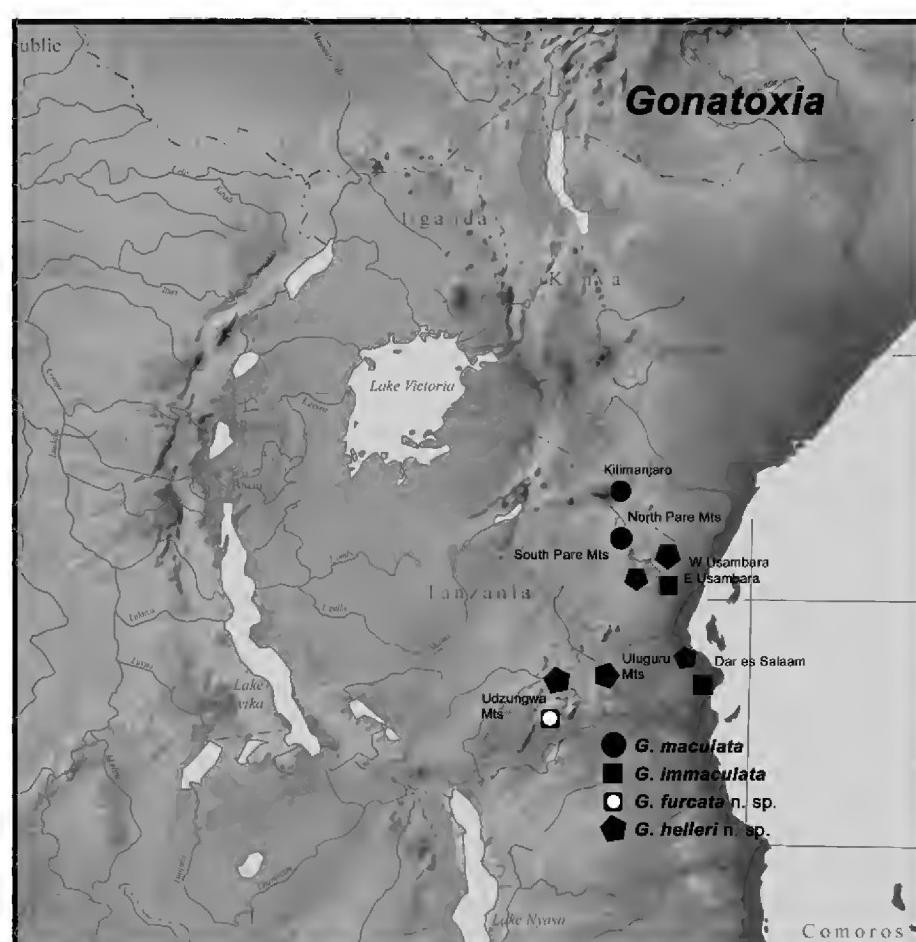


Figure 24. Map of East Africa with distribution of *Gonatoxia* species. *G. maculata* in Somalia is not indicated since locality information is insufficient.

clearly visible that the steep side of the asymmetric teeth are directed to the anal side (Fig. 18). This structure has been observed only in species in which the sound is produced during the closing movement of the tegmina as in most tettigonioids (Heller 1988). According to a hypothesis of Montealegre-Z. (2012) decreasing tooth intervals from anal to basal - as found in *Gonatoxia maculata*, *G.*

immaculata, *G. furcata* and the anal part of *G. helleri* - could indicate that sound is produced during the opening of the wings (called 'reversed' stridulation). However, the structure of the teeth strongly suggests a 'normal' sound production and questions the usability of inter-tooth intervals for documenting 'reversed' stridulation.

Chromosomes and evolution

The four species examined in this study revealed a remarkable variability in chromosome numbers and morphology. Patterns of chromosome evolution in this genus are very interesting and differ from the ancestral/model karyotype ($2n = 31$ in the male with acrocentric chromosomes) found in most tettigoniids (e.g. Warchałowska-Śliwa 1998) and most other African Phaneropterinae genera, e.g. *Altihoratosphaga*, *Horatosphaga*, *Monticolaria*, *Lunidia*, *Parapryrrhicia* or *Tropidonotacris* (Hemp et al. 2010a, b; 2014; 2016). The ancestral chromosome number is reduced to $2n = 29$ in *G. maculata* and *G. immaculata*, similar to *Eurycorypha* species (five species investigated so far; Hemp et al. 2013c) and *Plangia* (Hemp et al. 2015). This reduced chromosome number probably is the result of one tandem fusion. In *G. furcata* sp. n. the chromosome set is reduced to $2n = 27$ ($FN = 29$) probably by Robertsonian translocation, whereas an unexpected karyotype with only 7 chromosomes (in males) was revealed for *G. helleri* sp. n. Up to now such an exceptionally low chromosome number was not found in any tettigoniid species. Typical for the karyotype and also for the different karyomorphs of this species are very large autosomes compared to all other species of this genus, obviously caused by multiple rear-

rangements. Such significant differences in chromosome numbers and the morphology very likely resulted from successive tandem and Robertsonian fusions in various combinations. Our cytotoxic studies indicate that dramatic chromosomal rearrangements took place during speciation of *G. helleri* sp. n. which is one of the most wide-spread species of the genus so far. Detailed karyotype analyses of *Gonatoxia*, especially for *G. helleri* sp. n. using classic and molecular cytogenetics methods will be given by Warchałowska-Śliwa et al. (in prep).

Conservation and bioindication

Gonatoxia species were rarely collected, partly because they are nocturnal species, well camouflaged in the tree layer of forests and seasonal. But they are rarely collected partly also because they occur in habitats that are vanishing rapidly and also never had a large extension formerly. *Gonatoxia maculata* was only caught in deciduous dry forests and a vegetation type which was called “Obstgartensteppe” = orchard steppe by the Germans, since the trees are scattered and resemble superficially fruit trees planted in an orchard. Both vegetation types are rapidly vanishing in East Africa. The North and South Pare Mountains for example still harbour deciduous dry forests especially at their northern slopes. However, a rapidly increasing human population impact these forests by cutting, burning and using also steepest slopes as range land for life stock these days. The same holds true for the vegetation type “Obstgartensteppe” which is almost lost e.g. on Mt Kilimanjaro. Thus the presence of species such as *Gonatoxia maculata* serve as information about the vegetation types they are bound to, and therefore this species can be used as a bioindicator. The same was suggested for *Tropidonotacris grandis* occurring in same habitat types as *G. maculata* (Hemp et al. 2014). Another type of habitat rich in biodiversity and endemics, lowland wet forest, is indicated by *Gonatoxia immaculata*, *G. furcata* sp. n. and *G. helleri* sp. n. Coastal and lowland forests, once a contiguous belt along the Kenyan and Tanzanian coasts and at the foothills of mountain ranges and mountains are almost entirely cleared away today. Only few patches, mostly protected as forest reserves, are left. With them an unique flora and fauna disappear replaced by scrub and grassland harbouring some wide-spread species at the most. Thus passing e.g. between Segera at the northern coastal strip to Chalinze near Dar es Salaam in Tanzania forest has been completely cleared away over hundreds of square kilometers and barren land supports meagerly brittle life stock today. Reforestation programmes for the production of timber and fire wood could take away the pressure from the remaining few patches of coastal and lowland forest and should urgently be initiated.

Species such as *Gonatoxia*, *Parapyrrhicia* and *Tropidonotacris* may be used as bioindicators allowing to follow land cover changes over time since early collections reach back as far as the 18th century. Thus the evaluation

of old collections are precious archives providing multiple data to e.g. model scenarios of how land cover changed over time and to identify areas which once harboured habitats rich in biodiversity, e.g. for restoration programmes. Thus even few specimens of certain species as shown above for the Vienna collection holding a couple of specimens of different *Gonatoxia* species provides insight of the vegetation covering the area more than 100 years ago.

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Hidden species within the genus *Ocys* Stephens: the widespread species *O. harpaloides* (Audinet-Serville) and *O. tachysoides* (Antoine) (Coleoptera, Carabidae, Bembidiini)

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<http://zoobank.org/C09ADD81-A914-416A-9338-8525B0E35BB0>

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Abstract

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Beetles previously considered to be *Ocys harpaloides* (Audinet-Serville) from northern Africa, Spain, France, the United Kingdom, France, and Belgium belong to two species. These species can be distinguished using DNA sequences of 28S rDNA, 18S rDNA, COI, CAD, and topoisomerase I. A key, diagnoses, and images are provided to enable identification of specimens based upon characteristics of male and female genitalia, as well as microsculpture and other external structures. Through examination of the holotype of *Bembidium harpaloides* v. *tachysoides* Antoine, as well as designation of lectotypes of *Bembidion harpaloides* Audinet-Serville and *Ocys melanocephalus* Stephens, and designation of a neotype for *Tachis rufescens* Guérin-Ménéville, the valid names of the two species were determined to be *Ocys harpaloides* and *Ocys tachysoides* (Antoine).

Introduction

Among European carabid beetles of the tribe Bembidiini Stephens, *Ocys harpaloides* (Audinet-Serville, 1821) is one of the more distinctive, looking more similar to members of other tribes (for example, the trechine *Trechus* Clairville, 1806 or the tachyneine *Porotachys* Netolitzky, 1914) than to other bembidiines. As currently circumscribed, *Ocys harpaloides* is a common and widespread Mediterranean-Atlantic species, ranging from the Azores, Algeria and Morocco north to southern Norway, Britain and Ireland, and east to Italy, the Balkans and Greece (Lindroth 1992).

The only congener with which *O. harpaloides* is documented to coexist throughout much of this range is *Ocys quinquestriatus* (Gyllenhal), a species from which it can easily be distinguished by numerous morphological

characters (Lindroth 1974; see below). There are more than 20 additional species of *Ocys* Stephens; almost all of these are rare, and restricted to small geographic areas (e.g., Giachino and Vailati 2012; Magrini and Degiovanni 2009; Neri et al. 2011; Toledano and Wrase 2016; Vigna Taglianti 1994). Many of these distinctive, localized endemics occur at higher elevations in mountains in Spain, northern Africa, or Italy (Magrini and Degiovanni 2009; Neri, et al. 2011; Netolitzky 1942), or on islands (Magrini et al. 1998). However, one species similar to *O. harpaloides*, *Ocys tachysoides* (Antoine, 1933), has been reported from low elevation habitats in Morocco (Antoine 1933; 1955), Spain (Toribio 2013), and a montane region of Portugal (Sciaky 1998).

In Northern Ireland, two morphologically distinct forms of “*Ocys harpaloides*”, correlated with habitat, have been reported (Anderson et al. 2000): specimens found among

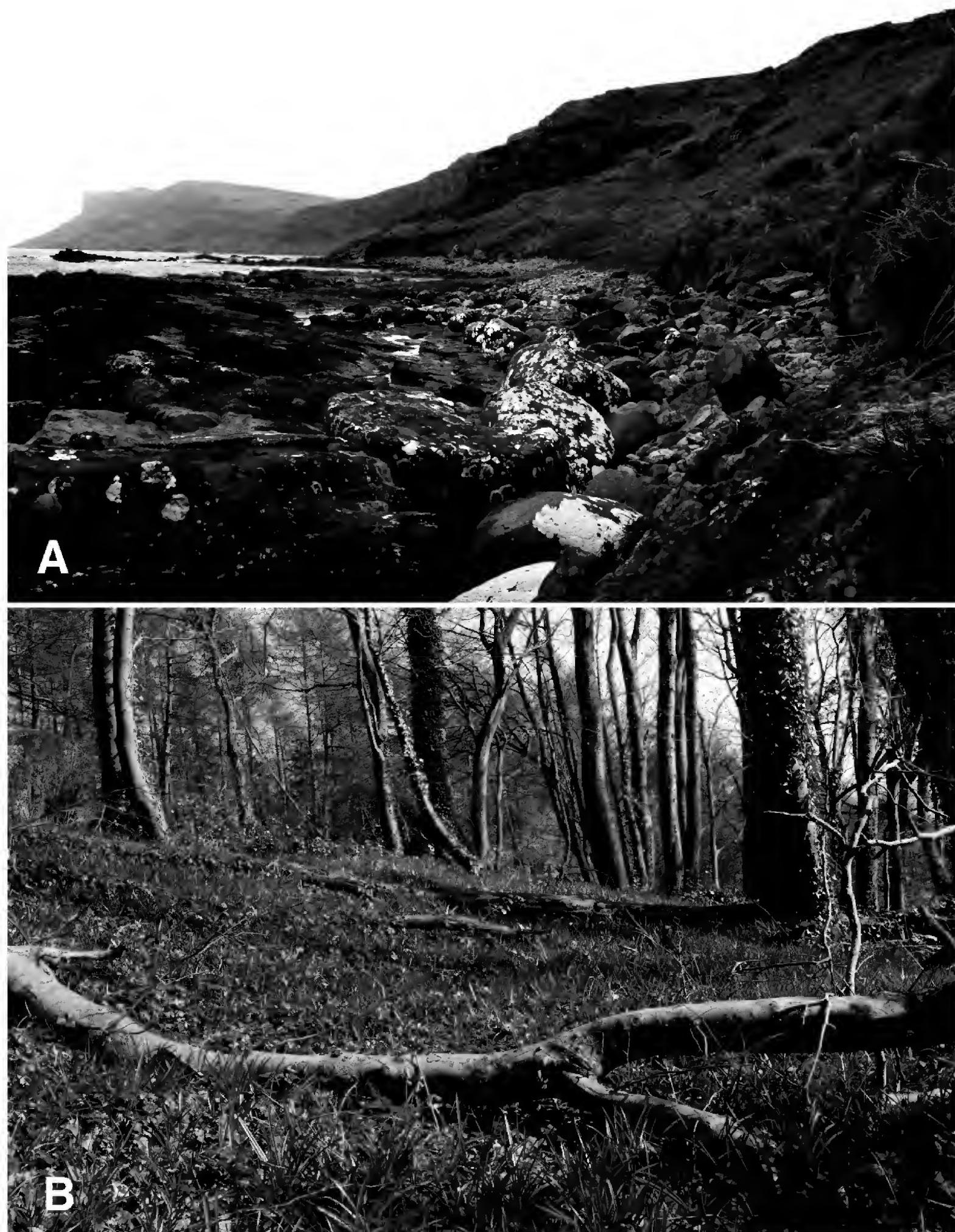


Figure 1. Habitats. **A:** East of Colliery Bay, Fair Head, Northern Ireland; **B:** Hollymount NNR near Downpatrick, Northern Ireland.

coastal rocks (Fig. 1A) are paler and larger (Fig. 2A), and those found in woodlands (Fig. 1B) are darker and smaller (Fig. 2B) (Anderson et al. 2000). Although this pattern might be a result of ecophenotypic variation, the observation suggested the possibility that two species could be hiding within "*Ocys harpaloides*". However, initial morphological investigations did not reveal additional, definitive differences (Anderson et al. 2000).

In 2011 we began an examination of the DNA sequences of these forms, and more detailed study of morphological variation. This revealed that two species were indeed

present in Northern Ireland, and elsewhere in the range of "*Ocys harpaloides*". As this paper was being prepared for publication, Raupach et al. (2016) reported the existence of two forms of "*Ocys harpaloides*" in Germany and France based upon the cytochrome oxidase I gene; these two forms correspond to the two species detailed here. In this paper, we document the differences between the two species, and through examination of types of the available names, show that the valid name of the second species is *Ocys tachysoides* (Antoine), which is much more widespread than previously believed.

Methods

Members of *Ocys* were examined from the collections listed below. Each collection's listing begins with the coden used in the text.

BMNH	The Natural History Museum, London
CTVR	Luca Toledano Collection, Verona, Italy
DE	Dominique Echaroux Collection, Etréchy, France
MNHN	Muséum National d'Histoire Naturelle, Paris
OSAC	Oregon State Arthropod Collection, Oregon State University
PB	Paolo Bonavita Collection, Rome, Italy
RAC	Roy Anderson Collection, Belfast, United Kingdom

Morphological methods. General methods of specimen preparation for morphological work, and terms used, follow Maddison (1993; 2008). Genitalia were prepared, after dissection from the body, by treatment in 10% KOH at 65 °C for 10 minutes followed by multi-hour baths of distilled water, 5% glacial acetic acid, distilled water, and then ethanol. Male genitalia were then mounted in Euparal between two small coverslips attached to archival-quality heavyweight watercolour paper, and, once dried, pinned beneath the specimen. For all type specimens except that of *Ocys melanocephalus* Stephens, genitalia were removed from Euparal through soaking in 100% ethanol, placed in small plastic vials containing glycerol, and pinned beneath the specimen.

Photographs of male genitalia were taken with a Leica Z6 and JVC KY-F75U camera using Microvision's Cartograph software for extended depth of field (EDF) processing; the images thus potentially have some artifacts caused by the EDF algorithm.

The following measurements were made:

Length: body length, from apex of the labrum to apex of the longer elytron.

GCR: gonocoxite ratio = gonocoxite 2 length / gonocoxite 1 length (Fig. 4)

Measurements were made either using Microvision's Cartograph software processing images from a JVC KY-F75U camera on a Leica Z6 lens, or on a Leica M3Z stereomicroscope with a Leitz graticule.

The density of the microsculpture lines on the left elytron was measured by counting the number of microsculpture lines that cross a 0.1 mm longitudinal line placed in the centre of the third elytral interval approximately 1/3 of the distance between the front and back of the elytron.

Taxon sampling for DNA studies. We obtained DNA sequence data for 15 *Ocys* specimens (Table 1), and combined these with results from the two *Ocys* specimens sequenced in Maddison (2012). For outgroups, we chose two or more species representing different lineages within each of the five largest genera of Bembidiina (*Bembidion* Latreille, *Asaphidion* Chaudoir, *Amerizus* des Gozis, *Sinechostictus* Motschulsky, and *Lionepha* Casey (Maddison, 2012)). The outgroup species are listed in Table 2.

DNA sequencing. Genes studied, and abbreviations used in this paper, are: **28S**: 28S ribosomal DNA (D1-D3 domains); **18S**: 18S ribosomal DNA (near full-length); **COI**: cytochrome oxidase I; **CAD**: carbamoyl phosphate synthetase domain of the *rudimentary* gene; **Topo**: topoisomerase I. In addition, sequences of the *wingless* gene and arginine kinase were acquired for specimens *Ocys harpaloides* 2759 and *Ocys tachysoides* 2758.

For all except specimen number 4606, DNA was extracted from specimens preserved in 95% ethanol using a Qiagen DNeasy Blood and Tissue Kit. Fragments for the seven genes were amplified using the Polymerase Chain Reaction on an Eppendorf Mastercycler Pro Thermal Cycler, using TaKaRa Ex Taq and the basic protocols recommended by the manufacturers. Primers and details of the cycling reactions used are given in Maddison (2012). The amplified products were then purified, quantified, and sequenced at the University of Arizona's Genomic

Table 1. Locality details for sequenced *Ocys* exclusive of *O. quinquestriatus*. Four-digit numbers at the start of each row are D.R. Maddison DNA voucher numbers. Specimen 0569 had been previously sequenced by Maddison (2012).

<i>Ocys harpaloides</i>	
2760	Northern Ireland: Colliery Bay, Ballycastle, Antrim, 55.2116°N 6.1910°W. 5.vii.2011. At grass roots on slope above high water mark. R. Anderson
2762	Northern Ireland: Colliery Bay, Ballycastle, Antrim, 55.2116°N 6.1910°W. 5.vii.2011. At grass roots on slope above high water mark. R. Anderson
2759	Ireland: Wexford, North Slob. 52.3546°N 6.4082°W. 20.vii.2011. Under driftwood on sandy beach. R. Anderson
0569	Belgium: Schorisse, Bos Ter Rijst. Approximately 50.78°N 3.69°E. 17.iv.1997. Temperate broadleaf forest. Konjev Desender
2937	Belgium: Schorisse, Bos Ter Rijst. Approximately 50.78°N 3.69°E. 17.iv.1997. Temperate broadleaf forest. Konjev Desender
2853	Belgium: Halve Maan, Oostende. 51.237°N 2.932°E. 23.ix.1995. Coastal salt marsh (non tidal). K. Desender.
4983	Spain: Sitges. 41.2383°N 01.8244°E. 9.ix.2006. W Maddison.
<i>Ocys tachysoides</i>	
2758	Northern Ireland: Belfast, Belvoir Forest. 54.5544°N, 5.9404°W. 10.iii.2011. Under bark dead alder and willow. R. Anderson
2761	Northern Ireland: Belfast, Belvoir Forest. 54.5544°N, 5.9404°W. 10.iii.2011. Under bark dead alder and willow. R. Anderson
2763	Northern Ireland: Belfast, Belvoir Forest. 54.5544°N, 5.9404°W. 10.iii.2011. Under bark dead alder and willow. R. Anderson
2898	Northern Ireland: Co. Down, Mount Stewart. 54.5491°N 5.6037°W. 12.x.2011. Under bark of sycamore/cedar/pine by sea. R. Anderson
2899	Northern Ireland: Co. Down, Murlough NNR. 54.2461°N 5.8330°W. 15.xi.2011. Under bark of sycamore, sandy wood near sea. R. Anderson
2936	Belgium: Moerzeke, De Kramp. Approximately 51.06°N 4.15°E. 1.iii.1999. Tidal freshwater marsh along the River Schelde. Konjev Desender
2938	Belgium: Kastel, Gespoelde. Approximately 51.05°N 4.16°E. 11.ix.1998 Tidal freshwater marsh along the River Schelde. Konjev Desender
4606	Germany: Nordrhein-Westfalen, Landkreis Unna, Selm-Bork, Lippeaue. 51.6533°N 7.4442°E. Under bark of <i>Salix</i> . K. Hannig

Table 2. Sampling of Bembidiina species. Four-digit numbers in the “#” column entries for *Ocys* are D.R. Maddison voucher numbers for sequenced specimens. Data for all non-*Ocys* specimens, as well as to specimens 1077 and 0569, were obtained from GenBank from previous studies (Maddison 2008; 2012; Maddison et al. 1999; Maddison and Ober 2011; Maddison and Swanson 2010; Wild and Maddison 2008), and more data about the specimens are presented in those papers. Locality details for *Ocys* specimens are given in Table 1 and in Maddison (2012). For each gene, GenBank accession numbers are listed.

	#	COI	28S	18S	CAD	Topo
<i>Bembidion chalceum</i> Dejean		EF649200	EF648892	EF648647	EF649431	EU677650
<i>Bembidion rapidum</i> (LeConte)		JN171095	EU677690	JN170224	EU677543	EU677642
<i>Bembidion transversale</i> Dejean		GU454797	EU677688	JN170242	EU677541	EU677639
<i>Bembidion variegatum</i> Say		JN171131	JN170458	JN170245	JN170937	JN171310
<i>Asaphidion curtum</i> (Heyden)		JN170977	GU556078	AF002792	JN170736	JN171163
<i>Asaphidion yukonense</i> Wickham		JN170979	JN170273	JN170139	EU677540	EU677638
<i>Amerizus wingatei</i> (Bland)		JN170974	JN170267	JN170136	JN170732	JN171160
<i>Amerizus (Tiruka)</i> sp.		JN170972	JN170265	JN170134	JN170730	JN171158
<i>Sinechostictus elongatus</i> (Dejean)		JN171152	JN170479	JN170260	JN170965	JN171332
<i>Sinechostictus (Pseudolimnaeum)</i> sp. 3		JN171150	JN170474	JN170259	JN170960	JN171329
<i>Lionepeha erasa</i> (LeConte)		JN171141	JN170468	JN170252	JN170948	JN171320
<i>Lionepeha osculans</i> (Casey)		JN171143	JN170470	JN170254	JN170950	JN171322
<i>Lionepeha disjuncta</i> (Lindroth)		JN171142	JN170469	JN170253	JN170949	JN171321
<i>Ocys quinquestriatus</i> (Gyllenhal)	1077	JN171145	JN170472	JN170257	JN170954	JN171324
	0569		GU556103	JN170256	JN170953	
<i>Ocys harpaloides</i> (Audinet-Serville)	2759	KX907141	KX907154	KX907168	KX907176	KX907188
	2760	KX907142	KX907155		KX907177	KX907189
	2762	KX907143	KX907156		KX907178	KX907190
	2853	KX907148	KX907161		KX907183	KX907195
	2937	KX907152	KX907165			KX907199
	4983	KX907153	KX907166			
	2758	KX907144	KX907157	KX907169	KX907179	KX907191
<i>Ocys tachysoides</i> (Antoine)	2761	KX907145	KX907158		KX907180	KX907192
	2763	KX907146	KX907192		KX907181	KX907193
	2898	KX907147	KX907160		KX907182	KX907194
	2899	KX907151	KX907164			KX907198
	2936	KX907149	KX907162		KX907184	KX907196
	2938	KX907150	KX907163		KX907185	KX907197
	4606	KX907187	KX907175	KX907172	KX907186	KX907167

and Technology Core Facility using a 3730 XL Applied Biosystems automatic sequencer. Assembly of multiple chromatograms for each gene fragment and initial base calls were made with Phred (Green and Ewing 2002) and Phrap (Green 1999) as orchestrated by Mesquite’s Chromaseq package (Maddison and Maddison 2014; Maddison and Maddison 2015b) with subsequent modifications by Chromaseq and manual inspection. Multiple peaks at a single position in multiple reads were coded using IUPAC ambiguity codes.

For specimen 4606, RNA was extracted from an RNA-Later preserved specimen using a Qiagen RNeasy Kit and Trizol (Life Technologies). Isolation of mRNA was done with an NEBNext® Poly(A) mRNA Magnetic Isolation Module (New England BioLabs). The library was prepared using an NEBNext Ultra RNA (New England BioLabs) kit using 1000 ng of input RNA and NEB-Next Multiplex Oligos for Illumina (New England BioLabs). The finished library was quantified using a Qubit Fluorometer (Life Technologies) and fragment distribution characterized on a 2100 Bioanalyzer (Agilent Technologies). The library was then sequenced on an Illumina 2500 at the Oregon Health Sciences University’s Massively

Parallel Sequencing Shared Resource, with reads demultiplexed using CASAVA v1.8. The 100-base, paired-end run produced 36 million reads, which were assembled using CLC Genomics Workbench version 8.5, using the *de novo* assembly feature with default parameter values. The resulting assembly was converted to a blastable database using NCBI’s makeblastdb tool. Using the *Asaphidion yukonense* sequences from Maddison (2012) as query sequences, the specimen 4606 transcriptome was searched using nBLAST, yielding single contig sequences for 28S, 18S, and Topo. For CAD, three overlapping contigs were found; they were identical in the overlapping regions, and were merged into a single sequence. For COI, three contigs were found, one containing full-length COI; the other two short fragments could be eliminated from consideration because they BLASTed to non-bembidiines in GenBank or contained stop codons.

Sequences have been deposited in GenBank with accession numbers KX907141 through KX907199 (Table 2). All sequences fall into the “genseq-4” category (Chakrabarty et al. 2013).

Alignment and phylogenetic analysis. The appropriate alignment was obvious for COI, CAD, and Topo,

as there were no insertion or deletions (indels) evident in the sampled sequences. The two ribosomal genes were aligned by MAFFT version 7.130b (Katoh and Standley 2013), using the L-INS-i search option and otherwise default parameter values. No data were excluded from analyses, other than trimming of ends of sequences that were notably longer than others.

Models of nucleotide evolution were chosen with the aid of jModelTest version 2.1.7 (Darriba et al. 2012; Guindon and Gascuel 2003). Among the models supported by GARLI, the models chosen by the Bayesian Information Criterion were 28S: TVMef+G, 18S: SYM+I+G, COI: TIM1+I+G, CAD: TVMef+I+G, and Topo: TrN+G. Likelihood analyses of nucleotide data were conducted using GARLI version 2.0 (Zwickl 2006), as orchestrated by the Zephyr package of Mesquite (Maddison and Maddison 2015a). Twenty-five search replicates were employed for maximum likelihood trees, and 200 replicates for bootstrap analyses.

Results

There are two distinct clades in each of the five gene trees (Fig. 5): one clade contains all of the larger, paler specimens, and another contains all of the smaller, darker specimens. As outlined below in the taxonomic section, the valid name for the larger, paler specimens is *Ocys harpaloides* (Audinet-Serville), and the valid name for the smaller, darker specimens is *Ocys tachysoides* (Antoine). Based upon the arguments presented below in the Discussion, we consider these different species, and for simplicity's sake we will speak of them as different species in this section, and use their valid names. Likelihood bootstrap support for these two species is strong (Table 3), being above 90% in at least two of the well-sampled genes.

In COI, there are 11 sites at which three to six of the *O. tachysoides* (all specimens except 2899) show a secondary peak in chromatograms; there are three different sites at which 1 to 3 *O. harpaloides* (2759, 2760, 2853) have a secondary peak. The secondary peaks suggest an alternative version of COI, which is presumably a nuclear copy, or "numt" (Thalmann et al. 2004), thus causing some uncertainty about the source of our sequenced COI. However, in spite of the uncertainty, the gene tree clearly supports two distinct species (Fig. 5).

A detailed examination of differences between and within each of these two species also reveals many sites at which they differ (Table 4). There are six fixed amino-acid differences between the two species across the three protein-coding genes.

Table 3. Support for the monophyly of each of the two species in data for each gene. Numbers shown are maximum likelihood bootstrap percentages.

Clade	28S	18S	COI	CAD	Topo
<i>O. harpaloides</i>	100	100	100	95	95
<i>O. tachysoides</i>	100	100	84	63	100

Table 4. Variation observed in the DNA sequences between and within species. The number of specimens examined per species ranged from 3 to 5, with each species represented by 2 to 3 localities. "nuc": nucleotides; "aa": amino acids. The * indicates that one of the fixed differences is an extra base in *O. tachysoides* relative to *O. harpaloides*.

gene	fixed differences between species		sites varying within species		% nuc differences between species
	nuc	aa	nuc	aa	
28S	22*	-	1	-	2.1-2.2
18S	15	-	1	-	0.9
COI	50	2	9	0	7.2-8.4
CAD	5	1	6	0	0.50-1.0
Topo	16	3	0	0	2.2

Table 5. Morphological features and habitats of the sequenced specimens. "Disc colour" refers to the colour of the elytral disc relative to the apex and lateral margins. Male genitalic type A is that shown in Fig. 6A, B, and genitalic type C is that shown in Fig. 5C, D; FA refers to female genitalia type shown in Figs 8A and 9A.

	Region	Disc colour	Genitalic type	Habitat
<i>O. harpaloides</i>	Northern Ireland	paler	A	ocean shore
<i>O. harpaloides</i>	Northern Ireland	paler	A	ocean shore
<i>O. harpaloides</i>	Republic of Ireland	paler	A	ocean shore
<i>O. harpaloides</i>	Belgium	slightly paler	FA	broadleaf forest
<i>O. harpaloides</i>	Belgium	slightly paler	A	coastal salt marsh
<i>O. harpaloides</i>	Belgium	± dark	A	broadleaf forest
<i>O. harpaloides</i>	Spain	paler	A	open woodland
<i>O. tachysoides</i>	Northern Ireland	dark	C	woodland
<i>O. tachysoides</i>	Northern Ireland	dark	C	woodland
<i>O. tachysoides</i>	Northern Ireland	dark	C	woodland
<i>O. tachysoides</i>	Northern Ireland	dark	C	woodland
<i>O. tachysoides</i>	Belgium	dark	C	freshwater marsh
<i>O. tachysoides</i>	Belgium	dark	C	freshwater marsh
<i>O. tachysoides</i>	Germany	dark	C	woodland

Morphological characteristics were in general correlated with DNA sequences. All five males in the *Ocys harpaloides* clade in Fig. 5 had genitalia matching those shown in Fig. 6A, B, and all seven males in the *Ocys tachysoides* clade had genitalia matching Figs 6C, D (Table 5). Irish populations also had the colour of the elytral disc correlated with the gene tree clades, but the correlation was not as clear in Belgium (Table 5).

On the island of Ireland, all three *O. harpaloides* clade males were found on the ocean shore, at two localities, whereas all five *O. tachysoides* clade males were found in woodland habitats, at three localities (Table 5). That distinction was not as evident on the mainland of Europe, as two of the *O. harpaloides* specimens from Belgium were found in a broadleaf forest, inland (Table 5).

Discussion

Our data show that specimens in northern Europe referred to “*Ocys harpaloides*” belong to two species. The DNA data alone strongly suggests that two species live in Northern Ireland and Belgium: the gene trees for two certainly unlinked genes (nuclear 28S and mitochondrial COI) show the same clades for specimens that broadly overlap in geographic range, with specimens of both forms sampled from each region. This pattern, combined with identical patterns for 18S, CAD, and Topo, indicates

that the two forms are not currently exchanging genes. This is confirmed by the correlated morphological traits, in particular the distinctive male genitalia.

Toribio (2013) recognized these two species in populations in southern Spain and Morocco, but did not recognize that *O. tachysoides* was as widespread as *O. harpaloides*.

By comparing our sequences with those presented by Raupach et al. (2016), we have confirmed that the two COI forms they documented correspond to *O. harpaloides* (their French specimens) and *O. tachysoides* (their German specimens).

Taxonomic section

The following key allows one to identify *Ocys* specimens from much of Europe, outside of those regions containing localized endemics (that is, outside of higher elevations in mountains in Spain, northern Africa, or Italy (Magrini and Degiovanni 2009; Neri et al. 2011; Netolitzky 1942), on islands (Magrini et al. 1998).

- 1 Pronotum with obtuse and rounded hind angles, with the hind margin protruding posteriorly in the middle relative to the hind angles; colour dark brown with bluish or greenish reflections *Ocys quinquestriatus* (Gyllenhal)
- Pronotum with sharp hind angles, approximately a right angle, with the hind margin more or less straight; colour without notable metallic reflections 2
- 2 Elytra rufous or brown, in most specimens paler centrally with darker apical and lateral margins. Microsculpture of elytra consisting of more closely spaced, transverse lines with less of a tendency to form meshes (Fig. 7A, B). Aedeagus with ventral margin in most specimens bent downward toward the thinner apex; anterior sclerites of the internal sac more rounded; with a brush sclerite of normal size (Fig. 6A, B). Spermatheca more curved (Fig. 9A, B) *Ocys harpaloides* (Audinet-Serville)
- Elytra dark brown to black in colour, in some specimens paler along the suture, but entire discal region not paler than margins. Microsculpture of elytra consisting of less closely spaced, transverse lines with more of a tendency to form meshes (Fig. 7C, D). Aedeagus with ventral margin straighter, and apex wider, with a blunter tip; anterior sclerites of the internal sac more angulate; with a very small brush sclerite (Fig. 6C, D). Spermatheca straighter (Fig. 9C, D) *Ocys tachysoides* (Antoine)

Ocys harpaloides (Audinet-Serville, 1821)

Figs 2A; 3A; 6A, B; 7A, B; 8A; 9A, B; 10A, B; 11A, B

Bembidion harpaloides Audinet-Serville, 1821:78. Lectotype male, here designated, in the Dufour collection of the MNHN, examined (see Nomenclatural notes, below), with two labels: “5244” [handwritten], “LECTOTYPE Bembidion harpaloides Audinet-Serville 1821 designated 2016 D.R. Maddison and R. Anderson” [partly handwritten, with red lines around the border]. Type locality: Clavados, Bretagne, France.

Tachis rufescens Guérin-Ménéville, 1823:123. Type specimens lost (see below). Type locality as specified in the original description: an island on the Seine River (presumably Île Seguin or Île Saint-Germain), Meudon, France. Neotype male, here designated, in the MNHN, labeled “JUVISY Aval RD 4-VI-45 M. DEWAILLY” [partly handwritten], “Ocys harpaloides Serv. M. Dewailly det.” [partly handwritten], “NEOTYPE Tachis rufescens Guérin-Ménéville designated 2016 D.R. Maddison & R. Anderson” [partly handwritten]. This specimen is from Juvisy-sur-Orge, Essonne, France, which is 18km SE of Meudon; it was formerly housed in the collection of Mr. Dominique Echaroux.

Ocys melanocephalus Stephens, 1828:10. Lectotype male, here designated, in BMNH, examined, with six labels: “BRITISH ISLES J. Stephens Coll. BM 1853- 46”, “O melanocephalum” [handwritten], “♂”, “harpaloides det Netolitzky” [handwritten], “NHMUK010363535” [with matrix barcode], “LECTOTYPE Ocys melanocephalus Stephens designated 2016 D.R. Maddison and R. Anderson” [partly handwritten, with red lines around the border]. Type locality: British Isles.

Bembidium dubium Wollaston, 1857:23. Holotype female, in BMNH, examined. Type locality: Madeira. Junior primary homonym of *Bembidium dubium* Heer, 1838. Synonymy tentative, based primarily on the colour of the type.

Nomenclatural notes. Interpretation of Audinet-Serville’s name rests in part on discovery of his specimens, as his description is not sufficient to distinguish between the two species. Audinet-Serville notes that his specimen or specimens of *Bembidion harpaloides* are from “M. de Brébisson”, presumably the botanist Louis Alphonse de Brébisson. Audinet-Serville’s Coleoptera specimens were acquired by Léon Jean Marie Dufour (Thierry Deuve, pers. comm.), whose collection was incorporated into the



Figure 2. Live *Ocys*. **A:** *Ocys harpaloides* (Benderg Bay, Co. Down, Northern Ireland); **B:** *Ocys tachysoides* (Barnett's Demesne, Belfast, Northern Ireland).

Muséum National d'Histoire Naturelle in Paris. In March 2016, David H. Kavanaugh searched for several hours for the type series of *Bembidion harpaloides* Audinet-Serville in Dufour's collection at the MNHN, with help from Azadeh Taghavian. The following notes are in part from Kavanaugh (pers. comm.). Dufour's collection is well-organized, and in the section containing bembidiines, there is only one box with *Ocys*. It contains four pins with *Ocys* specimens. These are housed under the heading “*Bembidion (Tachys) rufescens*”, a name in use around that time for this complex (e.g., Dejean 1831). In that region of the box, there are no additional pin holes, suggesting that there have been no specimens of *Ocys* removed from Dufour's collection. The four pins contain a total of eight specimens: the first two pins contain one specimen each, the third pin houses five specimens, each on a separate card, and the last pin houses a single specimen. The last

specimen can be excluded from consideration, as its label contains a locality (“Carcassonne”, in southern France) that differs from the locality stated by Audinet-Serville. The other three pins each have one or two labels: the first specimen has a label that apparently contains the number 249; the second the number 5244, and the remaining pin has two labels, one with a small amount of indecipherable text, the other with the number 124. All of the *Ocys* in Dufour's collection belong to this species, as determined by colour pattern and microsculpture. In addition, the first two are males, and dissection revealed genitalia that match genitalic type A (i.e., as in Fig. 6A, B). The labels on the three pins are in different handwriting, and the pins themselves differ in structure. Thus, it appears as if the three came from different sources, and likely only one of them represents authentic Audinet-Serville material. According to Antoine Mantilleri (Thierry Deuve, pers.

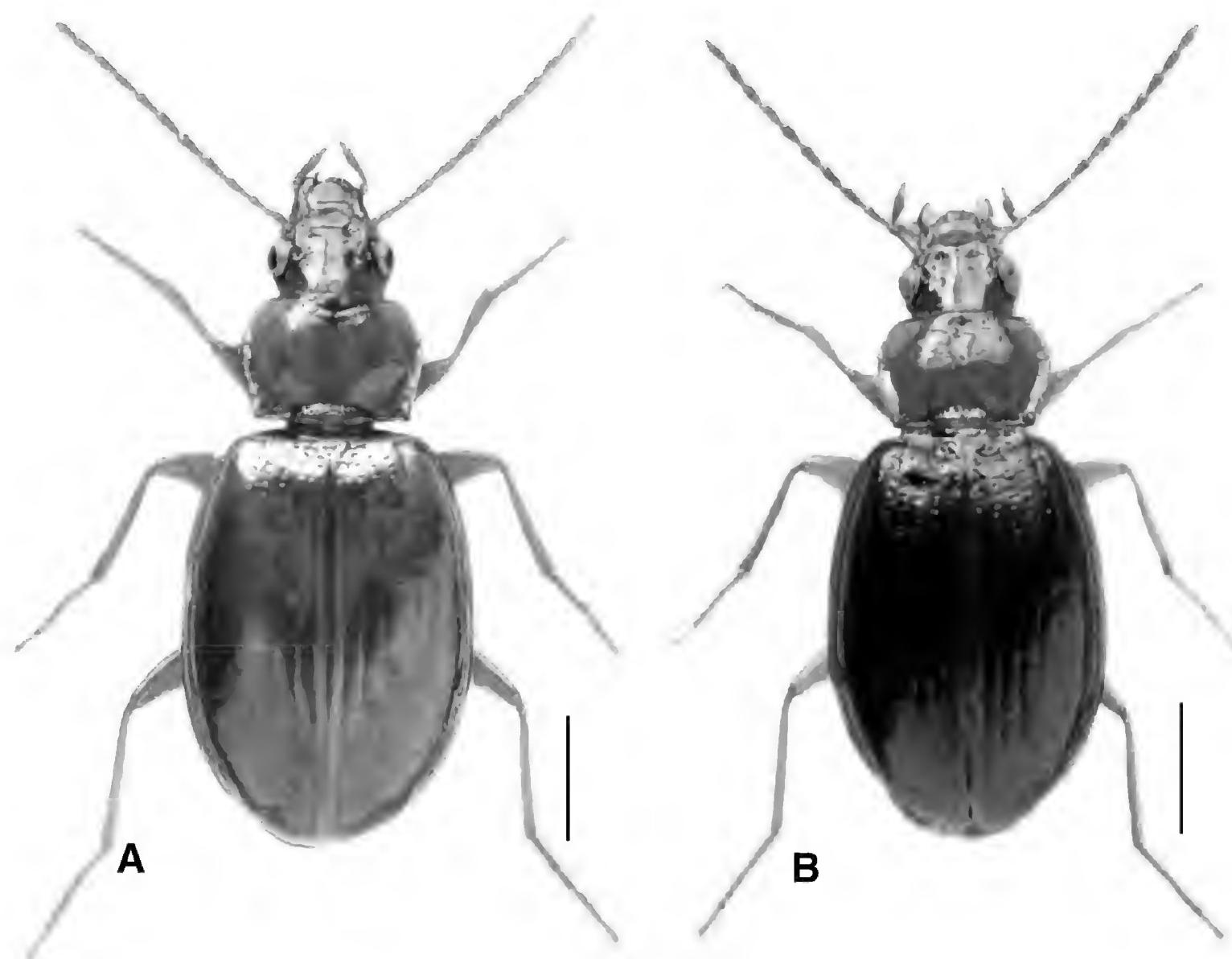


Figure 3. Habitus. **A:** *Ocys harpaloides* (Rinagree Point, Co. Londonderry, Northern Ireland); **B:** *Ocys tachysoides* (Annadale House, Belfast, Northern Ireland). Scale bars indicate 1 mm.

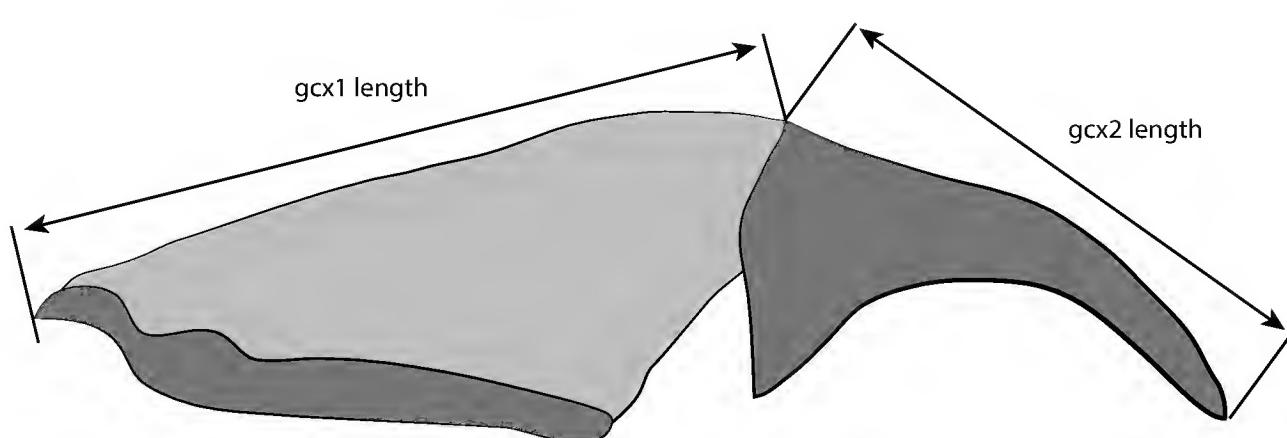


Figure 4. Diagram of gonocoxite of a female *Ocys* showing measurements taken.

comm.), the handwriting on the first specimen is likely that of Dufour. This suggests that the first specimen is not an authentic Audinet-Serville specimen, but rather an original Dufour specimen; however, it is possible that Dufour added a label to the specimen after having acquired Audinet-Serville's collection. The writer of the other labels is not known. We could discover no information about Audinet-Serville's handwriting, other than a single example of his signature, and thus we do not know if any of the labels might have been written by him, or whether they may have been added by later researchers. Thus, it is not clear which specimen on the three candidate pins is Audinet-Serville's, and it likely will never be determined with certainty. We consider the value in stabilizing the name more important than the uncertainty of the choice. As all of these specimens belong to the same species, as

the specimen on the second pin is a male in sufficient condition and with undamaged genitalia, and as there is hint that the specimen on the first pin is not an Audinet-Serville specimen, we have chosen the second specimen as the lectotype of *Bembidion harpaloides* Audinet-Serville.

The collection of Félix Édouard Guérin-Méneville was incorporated into the Chaudoir collection at the MNHN (Cambefort 2006) in the Chaudoir magasin. David Kavanaugh and Azadeh Taghavian searched for types of *Tachis rufescens* Guérin-Ménéville in the Chaudoir magasin. They found numerous *Ocys*, but every one could be eliminated as Guérin-Ménéville specimens through consideration of the labels, as all specimens had a mechanically printed label (against other Guérin-Ménéville specimens), and the labels specified a locality, collector, or collection that did not coincide

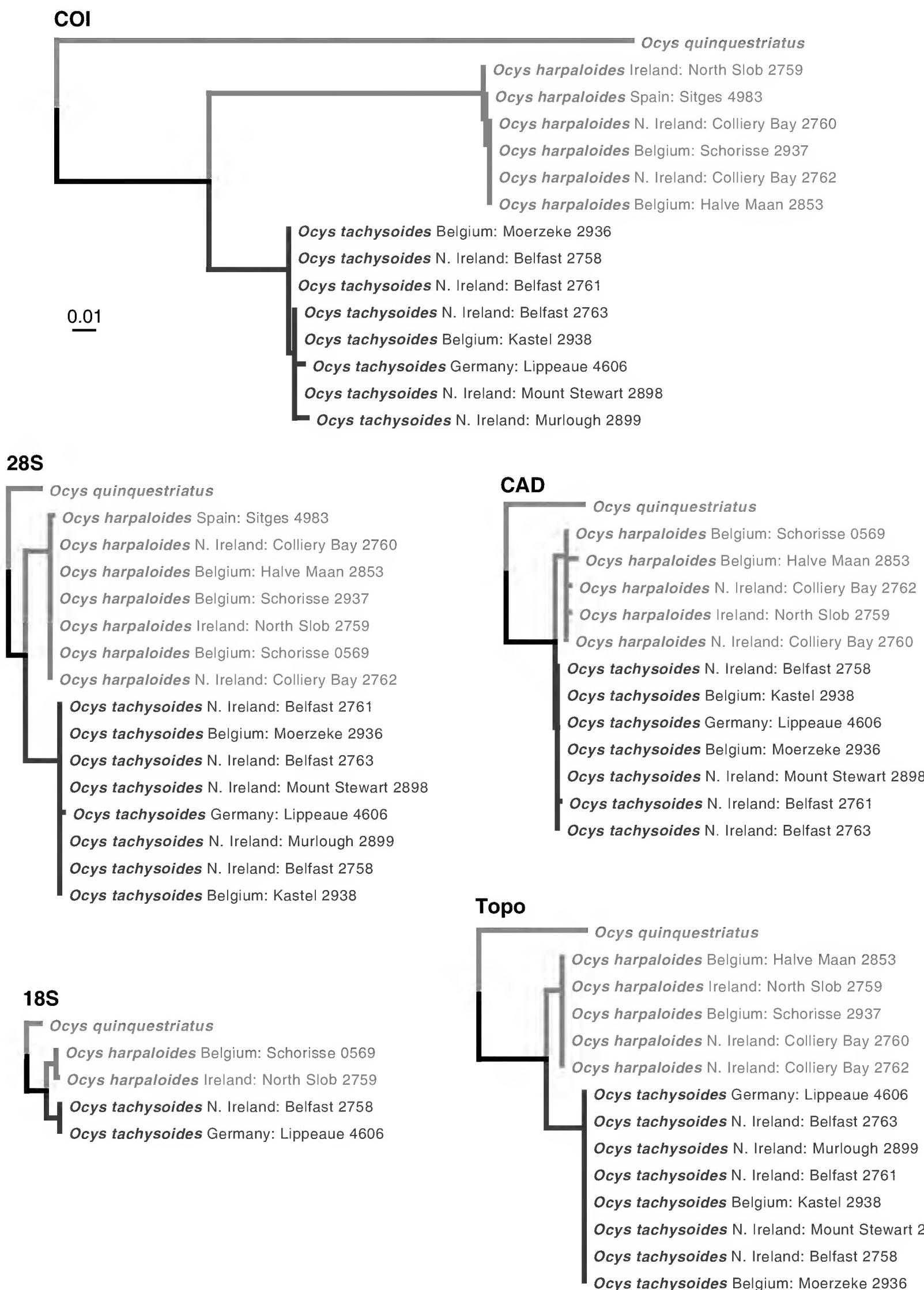


Figure 5. Phylogenetic trees of the five studied genes. Outgroups not shown. Branch length is shown proportional to relative divergence, as estimated by GARLI. The larger, paler specimens with genitalia as in Fig. 6A and B are shown in orange, and the smaller, darker specimens with genitalia as in Fig. 6C and D are shown in brown.

with those of the *Ocys* examined by Guérin-Ménéville (Kavanaugh, pers. comm.). The Guérin-Ménéville specimens of *Ocys* are thus lost. In the interests of stabilizing the nomenclature, we sought a neotype for *Tachis rufescens*. Within the MNHN, there are specimens

from three localities around Paris (Vaires, Chelles, and Chalifert). All of these specimens belong to the following species, *Ocys tachysoides* (Thierry Deuve, pers. comm.); we have confirmed this for the specimens from Vaires by examination of male genitalia. However, the

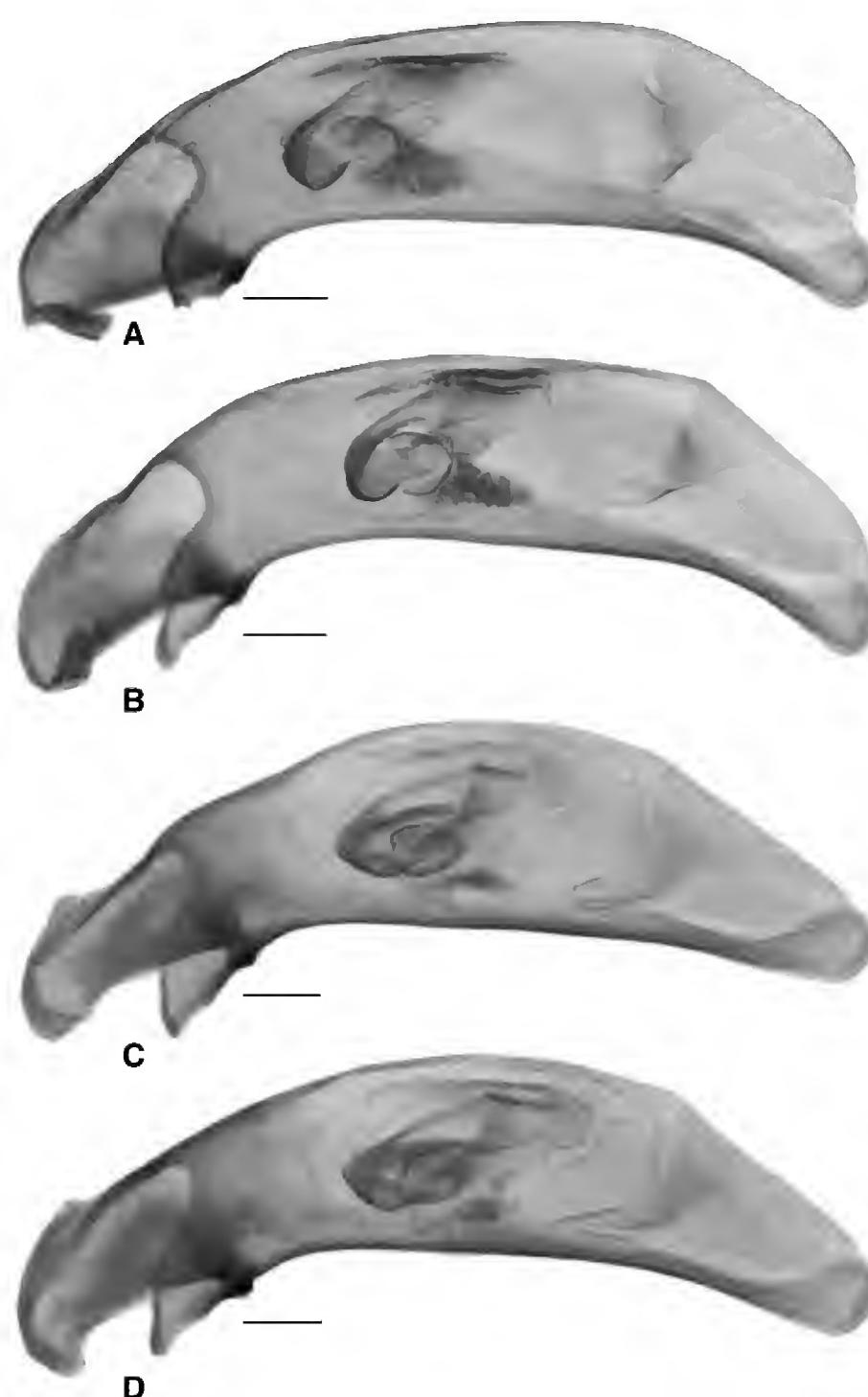


Figure 6. Male aedeagi. **A, B:** *Ocys harpaloides*, both from Colliery Bay, Ballycastle, Northern Ireland (A: voucher V100671, B: voucher V100670); **C, D:** *Ocys tachysoides*, both from Belvoir Forest, Belfast, Northern Ireland (C: voucher DNA2761; D: voucher DNA2758). Scale bars 0.1 mm.

lack of *Ocys harpaloides* in the twentieth-century specimens in the MNHN does not necessarily mean that the species was absent from Paris in 1823: in the 123 years that passed between the description of *Tachis rufescens* and the collection of the Vières specimens in 1946, the habitats around Paris may have changed. The possibility that *Ocys harpaloides* lived in Paris in the 1820s is made more likely by the presence, in the collection of Mr. Dominique Echaroux, of two series of specimens of *Ocys harpaloides* from just outside of Paris: one specimen from Bouray-sur-Juine and seven from Juvisy-sur-Orge. The latter is only 18 km SE of the type locality of *Tachis rufescens*. Thus, both species have lived in the general Paris area, and a specimen of either species could be designated as a neotype. However, designation of the Vières specimen, for example, would lead to *Ocys rufescens* as the name of the following species, with *O. tachysoides* as a junior synonym. This would change the name used for the following species in the Iberian Peninsula and Africa, where it is known as *O. tachysoides* (per Toribio 2013). In the interests of sta-

bility, we choose as neotype of *Tachis rufescens* one of the Juvisy-sur-Orge males; with this designation, *Tachis rufescens* is maintained as synonym of *O. harpaloides*.

In the BMNH, under “*melanocephalum*”, are seven specimens (four males, three females) in the J. Stephens collection, all with the label “British Isles J. Stephens Coll. BM. 1853 – 46”. We consider this to be the type series of *Ocys melanocephalus* Stephens. Three of the males in this series were dissected, and genitalia examined; they all match genitalic type A (i.e., as in Fig. 6A, D). We have chosen one of these specimens as the lectotype.

In the Wollaston collection of the BMNH, in Insecta Maderensis, Drawer 2, is a single teneral female, without a determination label. This specimen is presumed to be the holotype of *Bembidium dubium* Wollaston, 1854. Its colour suggests that it belongs to this species. However, the species membership of the type is of no nomenclatural importance, as the name is a junior primary homonym of *Bembidium dubium* Heer, 1838, itself a junior synonym of *Bemidion assimile* (Gyllenhal, 1810).

An additional name (*Carabus tempestivus* Panzer, 1799) is listed as a synonym of *O. harpaloides* by some authors (e.g. Stephens, 1828). However, this name is a synonym of *Trechus quadrifasciatus* (Schrank, 1781), as documented by Erichson (1837).

Diagnosis. Body length 4.2–6.1 mm (Toribio 2013 and our observations; average length of males 5.0 mm (n=5), of females 5.51 mm (n=5)). Head and pronotum a clear orange-brown; anterior and central part of elytra of the same colour, but sides and posterior region of elytra dark brown (Fig. 3), and with the epipleural gutter and suture yellow-brown. Microsculpture of elytral disc more transverse, with more close-set parallel lines and fewer meshes (Fig. 7A, B); density of microsculpture lines 25–26 per 0.1 mm (n=4 males). Hind margin of pronotum in most specimens straighter than in *O. tachysoides*, such that the hind margin is directed more or less laterally near the hind angles (Fig. 10A), occasionally with a slight emargination laterally (Fig. 10B). Elytra more parallel-sided, greatest width behind middle. Basal margin at shoulder slightly arcuate with a forward-directed concavity (Fig. 11A, B). Elytral striae 2 through 4 less marked in the apical third. Aedeagus with ventral margin bend slightly downward toward apex (Fig. 6A, B); apex more rounded. Anterior edge of central sclerite complex of internal sac more rounded; brush sclerite larger; dorsal membranes of internal sac darker. Gonocoxite relatively long (Fig. 8A), GCR=0.64–0.69 (average 0.67, n=5); spermathecal margin (opposite the efferent duct of the spermathecal gland) curved (Fig. 8A, B; n=5), with tip pointed toward duct of gland.

Geographic distribution (Fig. 12). In Africa, from Morocco, Algeria, and Tunisia. In Europe from Spain, France, Belgium, Italy, Ireland, and the United Kingdom. Examination of specimens in additional collections will likely show it to be more widely distributed.

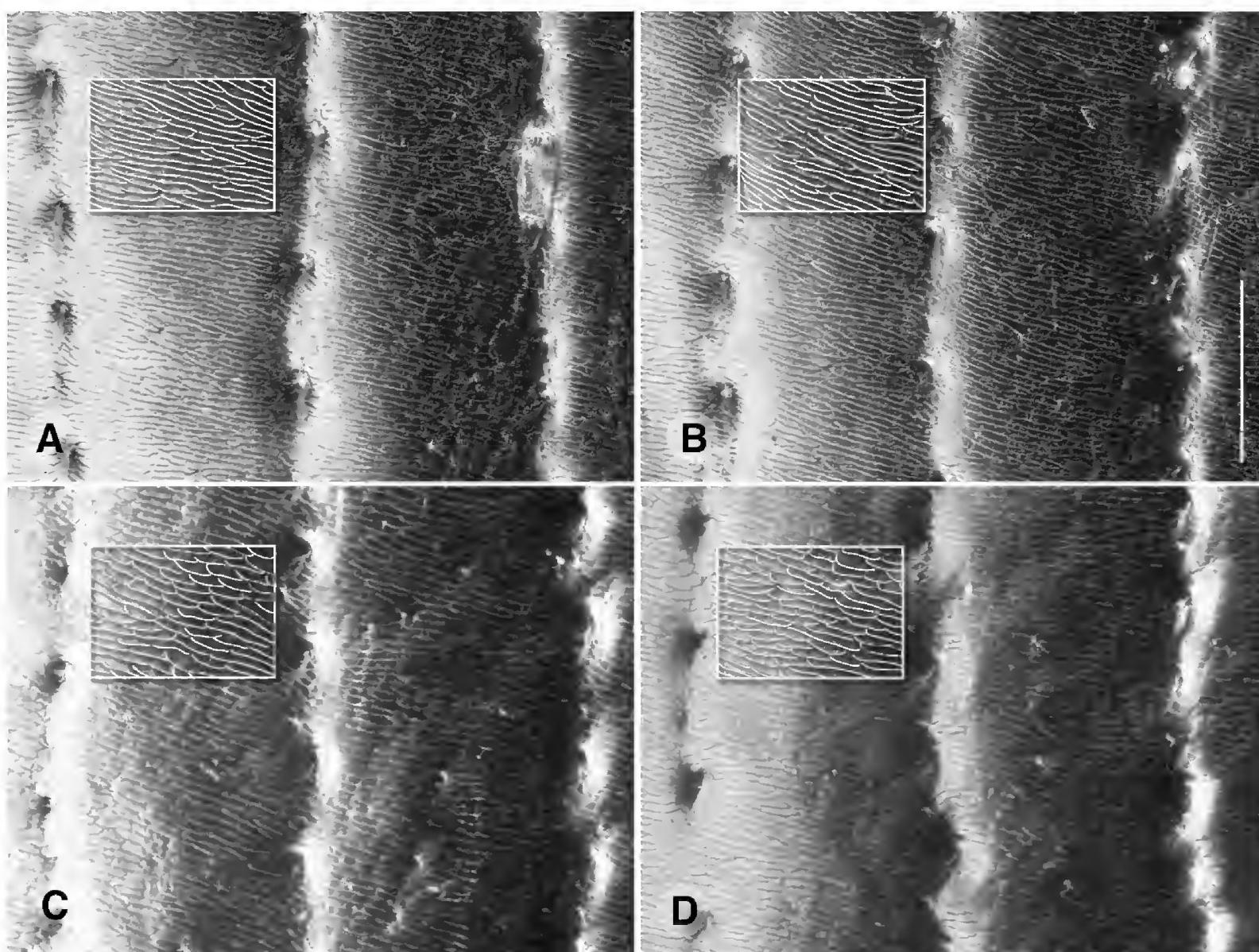


Figure 7. Microsculpture at center of disc of left elytron, third and fourth intervals. **A, B.** *O. harpaloides*, both from Colliery Bay, Ballycastle, Northern Ireland (A: voucher V100670, B: voucher V100672). **C, D.** *O. tachysoides* (C: Murlough NNR, Co. Down, Northern Ireland, voucher DNA2899, D: Mount Stewart, Co. Down, Northern Ireland, voucher DNA2898). Scale bar 0.1 mm.



Figure 8. Female genitalia. **A:** *O. harpaloides*, Bos Ter Rijst, Schorisse, Belgium, voucher DNA0569. **B:** *O. tachysoides*, Murlough NNR, Co. Down, Northern Ireland, voucher V100983. Scale bar 0.1 mm.

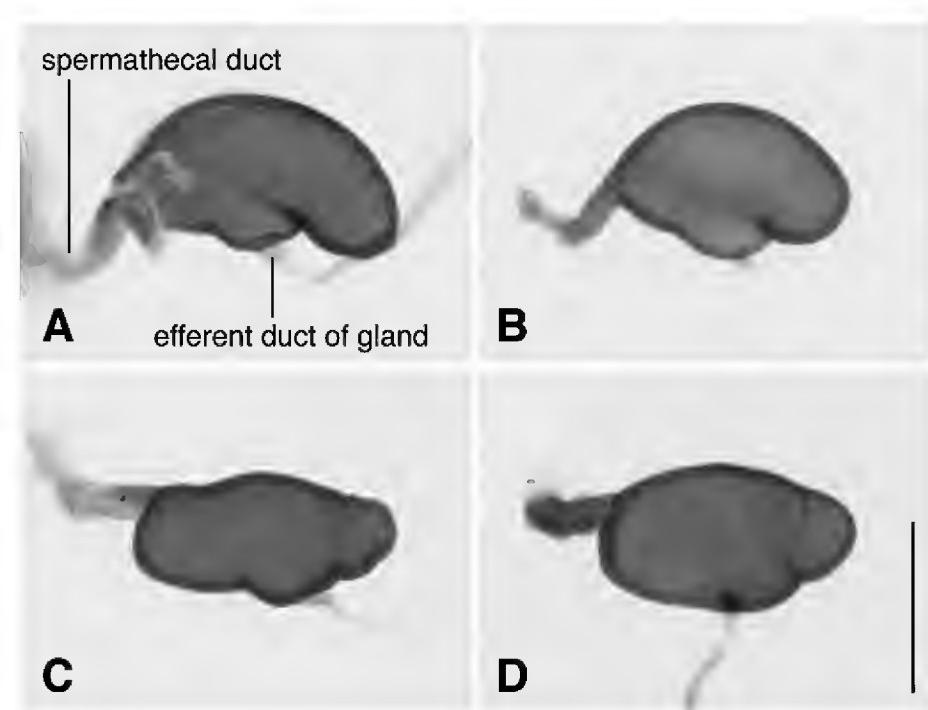


Figure 9. Spermatheca. **A, B.** *O. harpaloides* (A: Bos Ter Rijst, Schorisse, Belgium, voucher DNA0569, B: Beuda, Girona, Spain, voucher V100984) **C, D.** *O. tachysoides* (B: Murlough NNR, Co. Down, Northern Ireland, voucher V100983, D: Mount Stewart, Co. Down, Northern Ireland, voucher V100982). A bubble of air has been digitally removed from within the spermatheca shown in C. Scale bar 0.1 mm.

Specimens examined. In addition to type specimens, and those listed in Table 1, we examined specimens from Morocco: Tétouan (BMNH); Algeria (BMNH); France: Carcassonne (MNHN), Bouray-sur-Juine (DE); Spain: San Roque (BMNH), Beuda, Girona (OSAC), and Sant Carles de Peralta (RAC).

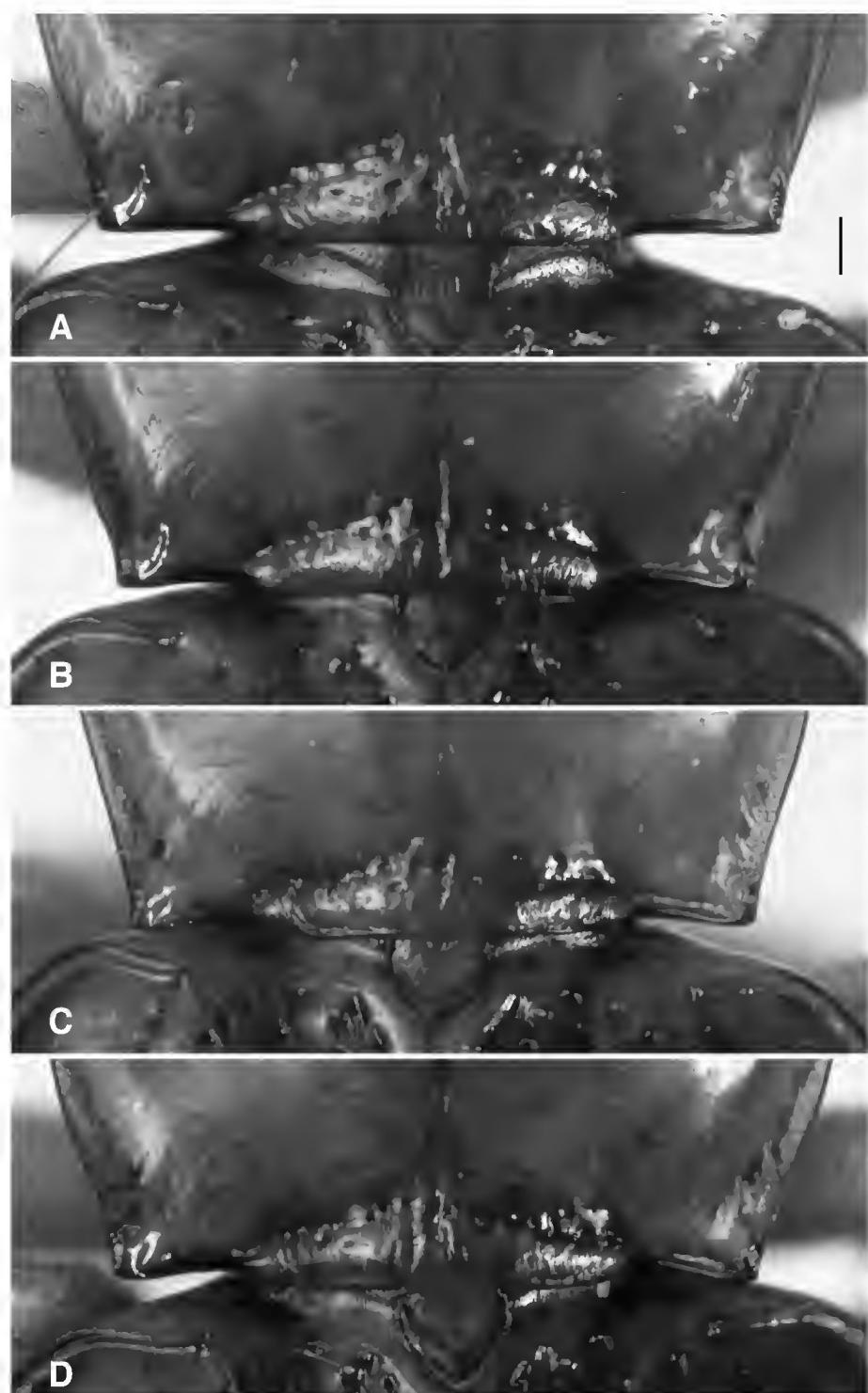


Figure 10. Hind margin of pronotum. **A, B,** *O. harpaloides* (**A:** North Slob, Wexford, Ireland, voucher DNA2759, **B:** Halve Maan, Oostende, Belgium, voucher DNA2853). **C, D,** *O. tachysoides* (**B:** Belvoir Forest, Belfast, Northern Ireland, voucher DNA2763, **D:** Murlough NNR, Co. Down, Northern Ireland, voucher DNA2899). Scale bar 0.1 mm.

Ocys tachysoides (Antoine, 1933)

Figs 2B; 3B; 6C, D; 7C, D; 8B, 9C, D; 10C, D; 11C, D

Bembidium harpaloides v. *tachysoides* Antoine 1933:79.
Holotype female, in the MNHN, examined, with three labels: “O. Nefifik (Maroc) Antoine I.1928” [partly handwritten], “Holotype” [handwritten on red paper], “tachysoides Antoine det. m.” [partly handwritten]. Type locality: Mouth of the Oued Nefifikh, east of Casablanca, Morocco (in the vicinity of 33.72°N, 7.34°W).

Nomenclatural notes. The type of *Bembidium harpaloides* v. *tachysoides* Antoine belongs to this species. We have examined external features of the holotype, including elytral microsculpture (which has a density of 21 lines per 0.1 mm), as well as shape of the spermatheca. Both second gonocoxites are broken in the holotype, and thus we were not able to measure their lengths.

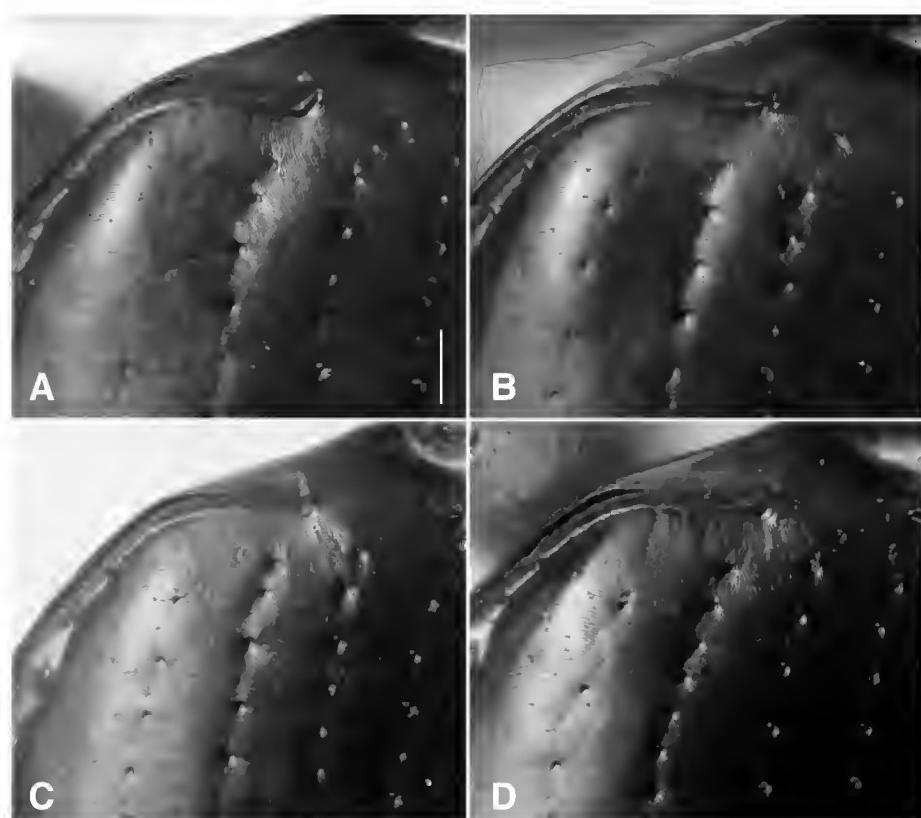


Figure 11. Left shoulder. **A, B,** *O. harpaloides* (**A:** North Slob, Wexford, Ireland, voucher DNA2759, **B:** Bos Ter Rijst, Schorisse, Belgium, voucher DNA2937) **C, D,** *O. tachysoides* (**B:** River Schelde, De Kramp, Moerzeke, Belgium, voucher DNA2936, **D:** Murlough NNR, Co. Down, Northern Ireland, voucher DNA2899). Scale bar 0.1 mm.

Diagnosis. Body length 4.0–5.8 mm (Toribio 2013 and our observations; average length of males 4.79 mm (n=7) of females 5.16 mm (n=7)). Head and pronotum a deep reddish-brown contrasting with the dark brown to blackish elytra (Fig. 3), only the epipleural gutters and sometimes sutures paler, light reddish-brown. Occasionally with a bluish lustre. Microsculpture of elytral disc less transverse, with more tendency to form sculpticells (Fig. 7C, D); density of microsculpture lines 20–21 per 0.1 mm (n=4 males). Hind margin of prothorax with a slight emargination laterally, such that the hind margin at the hind angles is directed posteriorly (Fig. 10C, D). Elytra less parallel-sided, greatest width around middle. Basal margin at shoulder in most specimens more or less straight (Fig. 11C), relatively few specimens slightly arcuate with a forward-directed concavity (Fig. 11D). Elytral striae 2 through 4 more marked in the apical third. Aedeagus with ventral margin bend more or less straight (Fig. 6C, D); apex less rounded, blunt. Anterior edge of central sclerite complex of internal sac angulate; brush sclerite smaller; dorsal membranes of internal sac paler, less evident. Gonocoxite relatively short (Fig. 8B), GCR=0.55–0.60 (average 0.58, n=5); spermathecal margin opposite the efferent duct of the spermathecal gland more or less straight (Fig. 8C,D; n=5).

Geographic distribution (Fig. 12). In Africa, known from Morocco (Antoine 1955). In Europe, from Portugal (Sciaky 1998), Spain (Toribio 2013), France, Belgium, Germany, and the United Kingdom. Examination of specimens in additional collections will likely show it to be more widely distributed.

Specimens examined. In addition to the type specimen, and those listed in Table 1, we examined specimens from France: Vaires (MNHN).

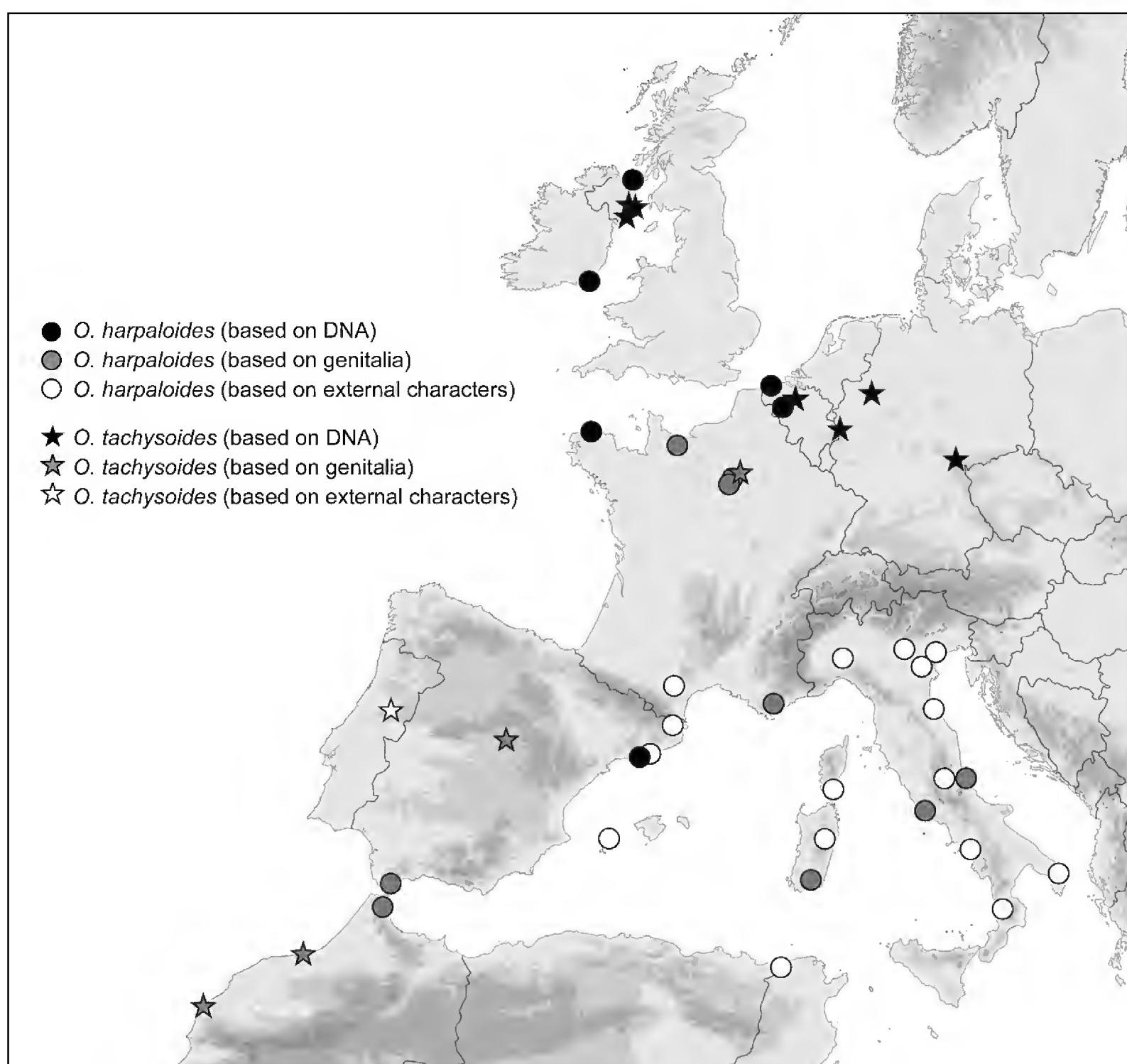


Figure 12. Distribution map of *Ocys harpaloides* and *O. tachysoides*. Only records of which we are confident are included. In addition to specimens we have examined, and those from Toribio (2013), Antoine (1956), and Sciaky (2009), we have included three publically available records from the Barcode of Life Database (<http://www.boldsystems.org>), corresponding to BOLD records GBCOU8213-14, GBCOU8667-14, and FBCOH116-12, as well as specimens identified by Luca Toledano and Paolo Bonavita in their collections (CTVR and PB, respectively) based upon images and diagnoses we provided to them.

Acknowledgements

We are extremely thankful to the individuals who worked so hard on our behalf as we were attempting to locate original Audinet-Serville and Guérin-Ménéville specimens at the Muséum National d’Histoire Naturelle, Paris, and to designate primary types for the associated names. Most importantly, Thierry Deuve patiently dealt with our many queries, examined numerous specimens, and visited Dominique Echaroux. His thoughtful responses, as we puzzled through the best approach to resolving the nomenclatural issues, were invaluable. Azadeh Taghavian’s help in this regard can also not go unmentioned. In addition, David Kavanaugh spent many valuable hours while in Paris personally looking for *Ocys* types, and we could have not completed the project without his help; we are also thankful for his advice as we considered the best path, and for hand-carrying the Audinet-Serville material back from Paris. Several others aided these efforts as well, and we wish to thank them: Antoine Mantilleri (for his

advice about Audinet-Serville material), and Paul Johnson (for providing copies of pages from Horn & Kahle). Finally, we wish to thank Mr. Dominique Echaroux, from Etréchy (Essonne, France), for providing specimens of *Ocys harpaloides* from his collection, and for allowing us to designate one of them as a neotype of *Tachis rufescens*.

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